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Fine-scale Climates and Evolution Alter Species Responses to Climate Change

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Fine-scale Climates and Evolution Alter Species Responses to Climate Change

Christopher. P. Nadeau, PhD

University of Connecticut, 2020

Predictions suggest that climate change could cause the extinction of up to a million species. However, scientists debate the accuracy of these predictions. In this dissertation, I explore whether often-ignored aspects of climate and biology alter predictions of climate change impacts. In Chapter 1, I show that studies predicting extinction risk under climate change ignore important aspects of climate by using climate data with coarse spatial and temporal resolutions. In Chapter 2, I propose that the degree to which climates vary over space and time in a region can predict the vulnerability of species to climate change. I suggest that populations living in regions with high spatial climatic variation (e.g., mountainous regions) should be less vulnerable to climate change and identify a tension between various effects of temporal climatic variation on climate change responses. In Chapter 3, I use *Daphnia magna* (an aquatic crustacean) in freshwater rock pools to evaluate whether populations from locations with greater temperature variation have adaptations that make them less vulnerable to climate change. Despite observing genetic variation and plasticity in a key thermal tolerance trait, I did not observe differences among populations as predicted. Moreover, I demonstrate a loss of evolutionary potential under warm temperatures, which could increase vulnerability. In Chapter 4, I map temperature variation at a sub-meter resolution in freshwater rock pools and demonstrate that this fine-scale temperature variation significantly alters predictions of climate change impacts on biodiversity. I also show that protecting cool microclimates might be a highly efficient means of conserving regional biodiversity under climate change. In Chapter 5, I use a literature review to suggest that

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evolution will likely alter species range dynamics under climate change, highlight potential conservation implications, and suggest a method for rapid learning in eco-evolutionary climate change biology. Last, in Chapter 6, I use lab experiments with archaea to provide experimental support of the community monopolization hypothesis, which is an eco-evolutionary dynamic that could increase extinction risk under climate change. This body of work increases our understanding of where and why species will be vulnerable to climate change and provides important insights for conservation biologists.

Fine-scale Climates and Evolution Alter Species Responses to Climate Change

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B.S., University of Arizona, 2009

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A Dissertation

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APPROVAL PAGE

Doctor of Philosophy Dissertation

Fine-scale Climates and Evolution Alter Species Responses to Climate Change

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Introduction

Climate change is already altering biological systems at all scales, ranging from genes to ecosystems (Scheffers et al. 2016). If greenhouse-gas emissions are left unchecked, the best predictions we have to date suggest that climate change could cause the extinction of up to a million species (Maclean and Wilson 2011, Urban 2015). However, scientists debate the accuracy of methods used to predict the impacts of climate change on biodiversity (Pearson and Dawson 2003, Hampe 2004, Beale et al. 2008, 2009, Araújo et al. 2009, Aspinall et al. 2009, Potter et al. 2013, Bennie et al. 2014). Two key factors underlie these debates.

First, predictions of climate change impacts on biodiversity often ignore important aspects of climate. For example, Potter et al. (2013) argued that predictions of species' climate change responses are often inaccurate because they ignore important aspects of climate by using climate data with a spatial resolution that is 10,000- and 1000-fold larger than the body size of focal animals and plants, respectively. However, Bennie et al. (2014) argued that matching the resolution of climate data to the body size of focal organisms is likely unnecessary because climate change studies are often interested in population-level responses. Bennie et al. (2014) did not compare the resolution of climate data to an estimate of the area encompassed by a population of focal species. Similarly, a growing body of research suggests that increasing the temporal resolution of climate data significantly alters predictions of climate change impacts on biodiversity (Early and Sax 2011, Nabel et al. 2013, Kingsolver and Buckley 2015).

Second, predictions of climate change often ignore important aspects of biology (Hampe 2004, Urban et al. 2016). For example, only one of 131 multi-species predictions included in a recent global synthesis of extinction risk under climate change accounted for evolution (Urban

2015, Urban et al. 2016). This oversight is likely because many reviews suggest evolution will occur too slowly to rescue species from extinction, except in very particular cases where species have short generation times and large population sizes (Bell and Collins 2008, Quintero and Wiens 2013, De Meester et al. 2018). Consequently, it may not be important to incorporate evolution into predictions of climate change impacts on biodiversity. But, what if evolution alters ecological responses to climate change even if it does not rescue species from extinction (Norberg et al. 2012, Thompson and Fronhofer 2019)? For example, even minor adaptation to warming on a species warm range margin could slow range shifts of other species and therefore alter climate change responses. In this case, accounting for eco-evolutionary dynamics might be critical to make accurate predictions.

In this dissertation, I explore how ignoring important aspects of climate could affect predictions of climate change impacts on biodiversity. More importantly, I ask whether we can use aspects of climate that are often ignored to predict where and why species will be vulnerable to climate change. I then suggest that evolution could alter species and community-level climate change responses even if evolution does not rescue species from extinction, and provide experimental evidence of such eco-evolutionary dynamics.

In Chapter 1, I ask whether studies predicting extinction risk under climate change are using climate data with biologically relevant resolutions, and explore where in the world using coarse resolution climate data is likely to reduce the accuracy of predictions.

Specifically, I determine the spatial and temporal resolution of climate data used in 131 studies predicting extinction risk for multiple species under climate change. I compare the spatial resolution of climate data to Wright's dispersal neighborhoods for plants, herpetofauna, birds, small mammals, and large mammals. Wright's dispersal neighborhood is a method to quantify

the area that encompasses a population. I also suggest that we should scale the temporal resolution of climate data to the generation time of focal species. I then provide a framework that partitions climate into three biologically relevant components: trend, variance, and autocorrelation. I use this framework to evaluate where in the world using coarse resolution climate data is likely to reduce the accuracy of extinction-risk estimates under climate change.

In Chapter 2, I propose that the degree to which climates vary over space and time in a region can predict the vulnerability of species to climate change. The vulnerability of a species to climate change is often partitioned into three components (Williams et al. 2008, Beever et al. 2016): exposure (i.e., the amount of climate change), sensitivity (i.e., the degree to which climate change affects fitness), and response capacity (i.e., the ability of a species to mitigate fitness reductions). Here, I propose that climatic variation in a region shapes landscapes, species traits, and genetic variation in those traits in predictable ways that alter all three components of vulnerability. Thus, we can use the degree of climatic variation in a region to predict climate change vulnerability. I provide seven predictions for how climatic variation could affect vulnerability, and use these predictions to identify where in the world species might be most vulnerable to climate change.

In Chapter 3, I evaluate whether species from locations with greater temperature variation have adaptations that make them less vulnerable to climate change. Temperate species are often predicted to be less vulnerable to climate change than tropical species, because temperate species have adapted a number of ways to deal with daily and seasonal temperature variation that is significantly reduced in tropical locations (Deutsch et al. 2008, Khaliq et al. 2014, Vasseur et al. 2014). Here, I use *Daphnia magna* (a small crustacean) in freshwater rock pools to evaluate whether this same logic can be applied at much finer (i.e., microgeographic)

spatial scales. I sample *D. magna* from freshwater rock pools that differ substantially in the degree of daily and seasonal temperature variation despite being separated by only 1 - 250 m. I use lab experiments to test whether a key thermal tolerance trait, plasticity, and genetic variation in that trait differ among pools as predicted by the amount of temperature variation in each pool. I also use a whole-ecosystem warming experiment in artificial rock pools to evaluate if potential differences in thermal tolerance among pools affects how *D. magna* responds to warming.

In Chapter 4, I ask whether using climate data with a sub-meter spatial resolution alters predictions of climate change impacts, and explore the value of conserving cool microclimates relative to another common biodiversity conservation strategy.

Microclimates are often overlooked in climate change biology because mapping fine-scale variation in climate is difficult in complex landscapes and ecosystems (Lenoir et al. 2017). Here, I map microclimates at a sub-meter resolution in 149 freshwater rock pools, where microclimates are determined by just a few key variables. I then compare the biological impacts of climate change between statistical predictions that use macroclimate and microclimate data. I evaluate whether microclimates reduce the impacts of climate change, and test whether protecting cool microclimates or protecting the currently most biodiverse locations is more likely to preserve biodiversity in the future. I also corroborate statistical predictions using a whole-ecosystem warming experiment in artificial rock pools.

In Chapter 5, I suggest that evolution will likely alter ecological responses to climate change, even if evolution does not rescue species from extinction, and explore the conservation implications. I review whether evolution could alter ecological responses to climate change on species range margins. I consider how multiple ecological and evolutionary processes could interact to affect species range dynamics under climate change. I first take a

single-species perspective, but then discuss how this perspective might change when multiple species are considered simultaneously. I also explore how practitioners might alter commonly recommended conservation strategies to account for eco-evolutionary dynamics under climate change. Last, I propose that resurveying historical studies that measured trait frequencies, the strength of selection, or heritabilities could be an efficient way to increase our eco-evolutionary knowledge in climate change biology.

Last, in Chapter 6, I experimentally test the community monopolization hypothesis, which has been proposed as an eco-evolutionary dynamic that could increase extinction risk under climate change. The community monopolization hypothesis proposes that adaptation of an early-arriving species to a location can reduce the colonization ability of a later-arriving species and therefore alter community assembly (a.k.a., an evolutionary priority effect). Recently, theoretical studies suggested that community monopolization by species on their warm range margins can prevent other species from shifting their distribution, and therefore increase biodiversity loss under climate change (Thompson and Fronhofer 2019). I provide one of the first experimental tests of the community monopolization hypothesis using experimental evolution and competition between two archaea species in a warm environment.

Climate change will undoubtedly cause large changes in biological systems worldwide. Improving predictions of these impacts is the first step in helping reduce extinctions and their effects on human wellbeing. By helping resolve debates over the importance of often-ignored aspects of climate and biology, my dissertation increases our understanding of where and why species will be vulnerable to climate change. In doing so, I also provide important insights into conservation strategies that could limit biodiversity loss under climate change.

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Chapter 1: Coarse Climate Change Projections for Species Living in a Fine-scaled World

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OPINION

Coarse climate change projections for species living in a fine-scaled world

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Abstract

Accurately predicting biological impacts of climate change is necessary to guide policy. However, the resolution of climate data could be affecting the accuracy of climate change impact assessments. Here, we review the spatial and temporal resolution of climate data used in impact assessments and demonstrate that these resolutions are often too coarse relative to biologically relevant scales. We then develop a framework that partitions climate into three important components: trend, variance, and autocorrelation. We apply this framework to map different global climate regimes and identify where coarse climate data is most and least likely to reduce the accuracy of impact assessments. We show that impact assessments for many large mammals and birds use climate data with a spatial resolution similar to the biologically relevant area encompassing population dynamics. Conversely, impact assessments for many small mammals, herpetofauna, and plants use climate data with a spatial resolution that is orders of magnitude larger than the area encompassing population dynamics. Most impact assessments also use climate data with a coarse temporal resolution. We suggest that climate data with a coarse spatial resolution is likely to reduce the accuracy of impact assessments the most in climates with high spatial trend and variance (e.g., much of western North and South America) and the least in climates with low spatial trend and variance (e.g., the Great Plains of the USA). Climate data with a coarse temporal resolution is likely to reduce the accuracy of impact assessments the most in the northern half of the northern hemisphere where temporal climatic variance is high. Our framework provides one way to identify where improving the resolution of climate data will have the largest impact on the accuracy of biological predictions under climate change.

Keywords: autocorrelation, grid size, impact assessment, spatial resolution, spatial scaling, temporal resolution, trend, variance

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Introduction

Global change is affecting the abundance and distribution of species, which is altering biological communities, ecosystems, and their associated services to humans (Parmesan & Yohe, 2003; Cardinale *et al.*, 2012; Kortsch *et al.*, 2015). These changes are expected to accelerate due to climate change (Maclean & Wilson, 2011; Urban, 2015). Accurately predicting biological responses to climate change is therefore necessary to help assess the potential impacts of climate change and guide policy designed to mitigate those impacts.

A growing number of studies indicate that the accuracy of climate change impact assessments is affected by the temporal and spatial resolution of climate data used to model climate change (Randin *et al.*, 2009; Early & Sax, 2011; Gillingham *et al.*, 2012; Bennie *et al.*, 2013; Lenoir *et al.*, 2013; Nabel *et al.*, 2013). For example, an average of 52% of high-elevation plant species was

predicted to become extirpated from two regions of Switzerland when assessments of extirpation used climate data with a coarse spatial resolution (19 by 13 km grid cells; Randin *et al.*, 2009). However, up to 100% of these species were predicted to persist when predictions were made using climate data with a fine spatial resolution (25 by 25 m grid cells; Randin *et al.*, 2009). The temporal resolution of climate data can also be important. For example, predictions made using coarse temporal climate data (i.e., two time periods 100 years apart) suggest that most western US amphibians will persist under climate change by shifting their range to track suitable climates (Early & Sax, 2011). However, decadal climate fluctuations could prevent many amphibians from accessing future suitable climates, which would significantly increase their extinction risk under climate change (Early & Sax, 2011).

The appropriate spatial and temporal resolution of climate data for climate change impact assessments requires further research, but is likely to depend on a

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few key factors. First, the appropriate spatial and temporal resolution of any study depends on the organism and process under investigation (Addicott *et al.*, 1987; Wiens, 1989; Levin, 1992; Bennie *et al.*, 2014). Organisms have adapted to regional climates by evolving unique life-history strategies, dispersal abilities, physiological tolerances, and behaviors that affect how they experience and respond to climate (Cohen, 1966; Levin *et al.*, 1984; Tewksbury *et al.*, 2008; Kearney *et al.*, 2009). Moreover, climatic variation at different resolutions (e.g., daily and seasonal) can interact to have complex effects on these traits (Chan *et al.*, 2016). Traits that are adapted to climate can make some species sensitive to fine-resolution weather events and microclimates, while allowing other species to moderate the effect of high climatic variability (Deutsch *et al.*, 2008; Buckley *et al.*, 2012). Consequently, the appropriate resolution of climate data will depend on key species traits, such as dispersal kernels and generation times, that have evolved in response to underlying abiotic and biotic complexity.

Second, the appropriate resolution of climate data is likely to depend on the climate within the focal region. Using coarse-resolution climate data in climates with low variation could have minimal effect on climate change impact assessments because the average climate used in coarse-resolution data accurately represents climates at finer resolutions (Woodcock & Strahler, 1987). Stochastic population dynamics are well represented by deterministic models when variation is low for the same reason (Chesson, 1981). However, in regions with high climate variation, important climate components could be masked when using coarse-resolution climate data (Randin *et al.*, 2009; Early & Sax, 2011).

Whether climate change impact assessments are using climate data with biologically relevant spatial and temporal resolutions is a matter of debate. A recent review compared the spatial resolution of species distribution models (i.e., the most common models used to evaluate the ecological impacts of climate change) to the body length of focal organisms (Potter *et al.*, 2013). The spatial resolution of species distribution models was approximately 10 000 times larger than the body length of focal animals and 1000 times larger than the body length of focal plants (Potter *et al.*, 2013). Potter *et al.* (2013) used this data to suggest a large spatial mismatch between the resolution of species distribution models and the scale at which species experience the environment.

Bennie *et al.* (2014) responded to this review, however, and suggested that the body length of focal organisms may not be the appropriate spatial resolution to consider when modeling species distributions. Bennie *et al.* (2014) suggest that the aim of species distribution

models is to predict the presence or absence of populations, and therefore, the area that encompasses population dynamics could be an appropriate spatial resolution to use in climate change impact assessments. They further suggest that the resolution required to map population presence and absence is similar to the resolution of climate data, although they do not provide data to support this claim.

In this article, we first show that many climate change impact assessments are using coarse-resolution climate data even when compared to the area that encompasses population dynamics. We also evaluate the temporal resolution of climate data used in climate change impact assessments. In the second part of the article, we suggest that climate can be partitioned into three components in both space and time – trend, variance, and autocorrelation – and we discuss the biological relevance of each component. We then demonstrate that using coarse climate data can misrepresent these three important climate components, which is likely to affect the results of climate change impact assessments. Last, we use these three climate components to map eight global climate regimes and identify where coarse climate data is most and least likely to misrepresent regional climates. This analysis guides where using finer resolution climate data could most improve the accuracy of climate change impact assessments.

The resolution of climate data used in climate change impact assessments

Methods

We recorded the spatial and temporal resolution of future climate projections used in a recently compiled list of 131 climate change impact assessments evaluating extinction risk for multiple species under climate change (Urban, 2015). We standardized the spatial resolution of climate data across studies by calculating the grid-cell area (km²) so that grid cells with unequal lengths and widths could be compared accurately to those with equal lengths and widths. For resolutions presented in degrees, we converted the latitudinal dimension to km using a factor of 111.325 km per degree and the longitudinal dimension using $\cos(\frac{\pi}{180}y)111.325$, where y is the approximate latitude of the center of the study area (Loarie *et al.*, 2009).

We also estimated the area of a population for 223 populations of 180 species. Some species were represented more than once if data from distinct studies or regions were available. We grouped species into five taxonomic groups: birds ($n = 45$), small mammals ($n = 13$), large mammals ($n = 14$), herpetofauna ($n = 58$), and plants ($n = 93$). This data allowed us to

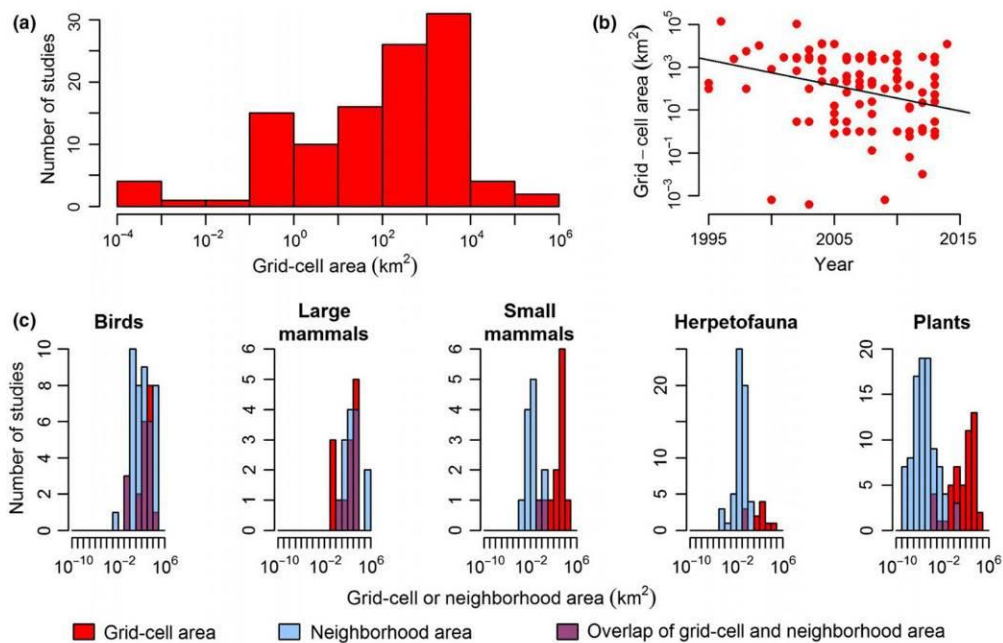


Fig. 1 (a) The spatial resolution of future climate projections used in 110 climate change impact assessments for all taxa and (b) the change in the spatial resolution used in climate change impact assessments over time. The trend in b is $-0.119 \text{ km}^2 \text{ per year}$ ($P = 0.002$). (c) The spatial resolution of future climate projections used in climate change impact assessments and the area of a population (i.e., the area of Wright's dispersal neighborhood) for species from five taxonomic groups.

evaluate whether grid-cell area was similar to the area that encompasses a population for each of the five taxonomic groups.

We estimated the area of a population for each species using Wright's dispersal neighborhood (Wright, 1946), one of the most common ways to estimate the area of a population (Crawford, 1982; Richardson *et al.*, 2014). Wright's dispersal neighborhood is the area that encompasses 86.5% of dispersal events and is therefore an area where individuals are likely to interact both ecologically and genetically. We estimated the dispersal-neighborhood area as $\pi(2\sigma)^2$, where 2σ is 1.6 times the mean or 1.7 times the median dispersal distance of a species (Urban, 2011). We obtained information on the mean or median dispersal distance of species using existing reviews on species dispersal distances (Sutherland *et al.*, 2000; Semlitsch & Bodie, 2003; Vittoz & Engler, 2007).

Results

The average spatial resolution (i.e., grid-cell area) of climate data from 110 studies using spatial climate data

was 3576 km^2 (SD = $16\,213 \text{ km}^2$, range = 0.0004 – $133\,506 \text{ km}^2$, Fig. 1a), which is equivalent to a square grid cell with approximately 60 km sides. The spatial resolution of climate data decreased by $0.119 \text{ km}^2 \text{ per year}$ ($P = 0.002$); however, the resolution varied substantially in any given year, including recent years (Fig. 1b). For example, in 2013, the resolution of climate data varied between 0.7 and 3098.3 km^2 .

The spatial resolution of climate data was similar to the area of a population for many birds and large mammals (Fig. 1c). However, the spatial resolution of climate data was orders of magnitude larger than the area of a population for many small mammals, herpetofauna, and plants (Fig. 1c). Hence, many climate change impact assessments for small mammals, herpetofauna, and plants used climate data with grid cells that could encompass multiple populations of the focal species, which could affect predictions of biological responses to climate change (Randin *et al.*, 2009; Gillingham *et al.*, 2012; Lenoir *et al.*, 2013).

The majority of studies (89%) that used temporal climate data compared the mean of weather variables in a historical period to the mean of the same weather

variables in one to three future periods (Fig. 2). This method ignores climate dynamics between the historical and future periods (Fig. 2). Two percent of studies used a linear change in climate between a historical and future period, which also ignores much of the climate dynamics between the historical and future time period (Fig. 2). Only 9% of studies used an annual or decadal resolution that captures some of the climate dynamics that could occur through time (Fig. 2).

These results suggest that many climate change impact assessments are using climate data that is not mapped at biologically relevant spatial or temporal resolutions. Next, we demonstrate that climate data can be partitioned into three biologically relevant components and demonstrate how using coarse-resolution climate data can misrepresent these components in climate change impact assessments.

Partitioning climate into three biologically relevant components

Climate can be partitioned into three components over both space and time: (i) trend, (ii) variance, and (iii) autocorrelation (Fig. 3). Climatic trend is a consistent increase or decrease in the mean of a weather variable (e.g., average annual temperature) over large temporal or spatial scales relative to biological scales (Box 1). For example, climate change is a temporal climatic trend and latitudinal and elevational gradients in climate are spatial climatic trends (Fig. 3). Climatic variance is the average

deviation of climate from the trend within a time period or region (Fig. 3). Climatic variance measures the degree of variability in a weather variable within a focal time period or area. Climates with high variance have a wide range of weather conditions within a focal time period or area (Fig. 3). Autocorrelation is a measure of the similarity of neighboring observations of a weather variable in time or space. Positive climatic autocorrelation measures the length of periods with similar weather over time and the size of climatically similar patches in space (Fig. 3). Long periods of similar weather and large patches of similar climate occur more often in highly autocorrelated climates or regions (Fig. 3). Climatic autocorrelation also measures the predictability of weather over time and climates in space. For example, in climates with low temporal autocorrelation, the weather in one time period will not accurately predict the weather in future time periods (Fig. 3b). Similarly, for climates with low spatial autocorrelation, the climate in one location will not accurately predict the climate in neighboring locations (Fig. 3a).

Climate change impact assessments have primarily focused on climatic trend. For example, the average rate of climate change has been associated with the magnitude of species range shifts under recent climate change (Chen *et al.*, 2011) and can affect the ability of species to adapt *in situ* (Lynch & Lande, 1993; Burger & Lynch, 1995; Burger & Krall, 2004). Spatial trends have facilitated range shifts under climate change by allowing species to track suitable climates as the climate changes (Chen *et al.*, 2011). A combination of temporal and spatial trend has

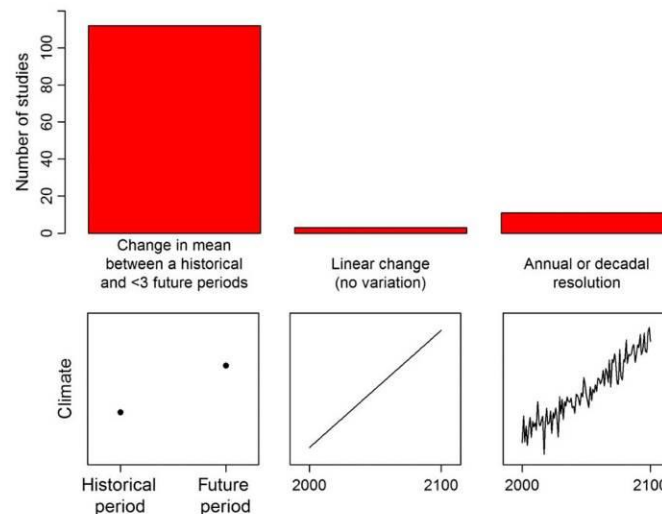


Fig. 2 The number of climate change impact assessments using three different temporal resolutions. The figures below each bar provide examples of the three temporal resolutions.

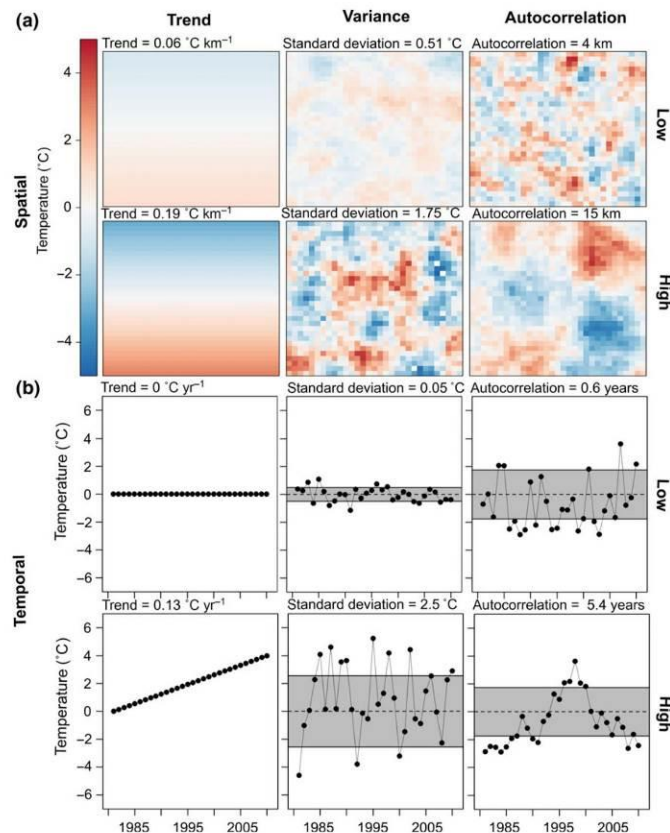


Fig. 3 Examples of (a) spatial and (b) temporal trend, variance, and autocorrelation. Examples with high and low values of each component are shown for contrast. Spatial trend is represented as a systematic change in the color from the top to the bottom of the plots. Spatial variance is represented by the range of colors in each plot, and spatial autocorrelation is represented by the size of similarly colored patches. The black points in the temporal plots represent estimates of mean annual temperature, the dashed line represents the temporal trend, and the gray shaded area represents temporal variance (± 1 SD). Temporal autocorrelation is represented by consecutive years with similar temperature measurements (e.g., on the same side of the trend line).

been used to estimate the rate that species will need to move to track suitable climates (Loarie *et al.*, 2009).

Climatic variance and autocorrelation have received much less attention in climate change impact assessments. However, environmental variance and autocorrelation (including climatic variance and autocorrelation) have long been known to affect population dynamics (Lande, 1993; Ripa & Lundberg, 1996; Benton *et al.*, 2002; Holt *et al.*, 2003; Drake & Lodge, 2004; Schwager *et al.*, 2006; Schreiber, 2010) and the ability of species to move across the landscape (With, 2002), coexist (Chesson & Warner, 1981; Caswell & Cohen, 1995; Chesson, 2000; Büchi & Vuilleumier, 2014), and adapt to local conditions (Lynch & Lande, 1993; Burger &

Lynch, 1995; Gomulkiewicz & Holt, 1995; Lande & Shannon, 1996; Burger & Krall, 2004; Holt, 2004; De Mazancourt *et al.*, 2008; Schippers *et al.*, 2014). For example, both theory and experiments suggest that time to extinction of closed populations decreases as the temporal environmental variance and autocorrelation increase (Ripa & Lundberg, 1996; Benton *et al.*, 2002; Drake & Lodge, 2004). Temporal environmental variance and autocorrelation can also increase the size of open populations (Holt *et al.*, 2003; Matthews & Gonzalez, 2007), which can affect the probability that a sink population will adapt to become a source (Holt, 2004). The well-known effects of temporal and spatial environmental variance and autocorrelation on ecological

Box 1 Scaling Climate Data to Focal Species

Two scaling factors will affect how climatic trend, variance, and autocorrelation are represented in both temporal and spatial climate data: the neighborhood size and the resolution (Chou, 1991). For space, the neighborhood size is the study area and the resolution is the grid-cell size (Fig. B1a). For time, the neighborhood size is the focal time period and the resolution is the time between observations (Fig. B1b).

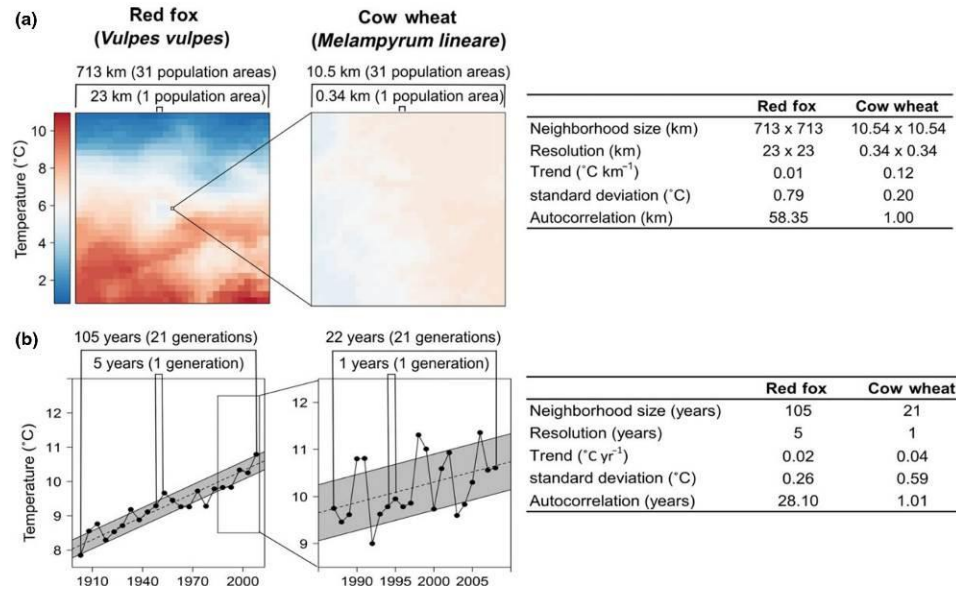


Fig. B1 Examples of (a) spatial and (b) temporal climate variation for species with different dispersal distances and generation times.

The definition and magnitude of climatic trend, variance, and autocorrelation can differ depending on the neighborhood size and resolution of the climate data. Consequently, the neighborhood size and resolution of climate data can greatly affect how climatic trend, variance, and autocorrelation are represented in climate change impact assessments.

Figure B1a provides an example of how the spatial neighborhood size and resolution can differ between two species with very different dispersal abilities: a mammal (Red Fox, *Vulpes vulpes*) with high dispersal ability and an annual plant (Cow Wheat, *Melampyrum lineare*) with low dispersal ability. We scaled the spatial resolution to the area that encompasses a population for the two species. We scaled the spatial neighborhood to include 15 population areas in each cardinal direction from the center cell. This spatial neighborhood includes the landscape cells that are most likely to influence the population in the center cell over 15 generations (i.e., landscape cells that individuals from the population in the center cell could access and landscape cells that could contribute immigrants to the center cell over 15 generations via natal dispersal).

The spatial resolution and neighborhood size is 68 times greater for the red fox than for the cow wheat (Fig. B1a). This difference in the spatial scaling between the two species results in differences in how the species might experience climate and thus respond to climate change. For example, cow wheat will experience higher spatial trend within its spatial neighborhood (Fig. B1a), suggesting that populations of cow wheat may need to move shorter distances to track suitable climates under climate change in this region. The spatial trend also differs in direction between the two species: temperature increases from north to south for the red fox and from southwest to northeast for the cow wheat (Fig. B1a). Hence, the direction of range shifts under climate change may differ between the two species in this region. The red fox will experience more spatial variance and autocorrelation in its spatial neighborhood, which increases the likelihood that local climate refugia will exist for red fox in this region (Randin *et al.*, 2009).

Figure B1b shows an example of how the temporal neighborhood size and resolution can differ between the same two species, which have different generation times. We scaled the resolution of the time series to one generation and the neighborhood size to include 21 generations.

The neighborhood size and resolution is five times greater for the red fox than for cow wheat. This difference in temporal scaling affects how each species is likely to experience climate change over time. Cow wheat will experience more temperature change (i.e., temporal trend) over the 21 generations (Fig. B1b). Consequently, cow wheat might need to adapt more or shift its range further per generation than the red fox to cope with climate change. Cow wheat will also experience more temporal variance and less temporal autocorrelation than the red fox. These differences in variance and autocorrelation can affect the ability of the species to shift their ranges and evolve adaptations to climate change (Burger & Lynch, 1995; Burger & Krall, 2004; Early & Sax, 2011).

Models that account for other traits and other important climate variables are necessary to determine whether differences in how the species experience climate will result in different responses to climate change. However, many studies suggest that differences in how species experience climate will affect their responses to climate change (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008).

and evolutionary dynamics suggest that climatic variance and autocorrelation will affect species responses to climate change.

Relatively few studies have specifically addressed how climatic variance and autocorrelation affect species responses to climate change. The few that do address these components demonstrate strong effects on outcomes (Randin *et al.*, 2009; Early & Sax, 2011; Gillingham *et al.*, 2012; Nabel *et al.*, 2013; Schiffrers *et al.*, 2013). For example, both spatial and temporal variance in the environment can maintain standing genetic variation that could allow species to persist under many decades of climate change (Kelly *et al.*, 2003; Yeaman & Jarvis, 2006) or slow the rate of evolutionary adaptation of species with dormant life stages (Rubio *et al.*, 2015). Also, the magnitude of climate change to which a species can adapt decreases as the temporal variance of the environment increases (Lande, 1993; Lynch & Lande, 1993; Burger & Lynch, 1995; Burger & Krall, 2004). Spatial and temporal climatic variance can also prevent species from tracking suitable climates (Canning-Clode *et al.*, 2011; Early & Sax, 2011; Bennie *et al.*, 2013; Nabel *et al.*, 2013).

More research is needed to determine how spatial and temporal climatic variance and autocorrelation will affect species' responses to climate change, but climatic variance and autocorrelation are likely important. Therefore, it is critical to ensure that these components of climate are accurately represented in models used to assess the impacts of climate change.

Where will coarse climate data affect the accuracy of impact assessments

To accurately represent climatic trend, variance, and autocorrelation in climate change impact assessments,

it is necessary to use climate data with biologically relevant spatial and temporal resolutions (Boxes 1 and 2).

The ability to scale climate data to the appropriate resolution for use in climate change impact assessments will be limited by the availability of fine-scale climate projections. Climate data generated by current atmospheric-ocean general circulation models can often be obtained with a fine temporal resolution (e.g., daily, hourly), but the spatial resolution is often in the order of 200 by 200 km (Intergovernmental Panel on Climate Change, 2014). This coarse spatial resolution is larger than the area that encompasses a population for most species (Fig. 1). Although advances in spatial downscaling are allowing researchers to use climate data with much finer spatial resolutions in climate change impact assessments (Hannah *et al.*, 2014), it is still difficult to obtain climate data with an appropriate resolution for many species. Hence, we need to understand where using coarse-resolution climate data is likely to have the biggest effect on predictions of biological responses to climate change.

The degree to which climatic trend, variance, and autocorrelation are misrepresented using coarse-resolution climate data depends on the magnitude of each climate component in the focal neighborhood (Woodcock & Strahler, 1987; Chou, 1991). For example, spatial climatic variance is likely to be highly underestimated using coarse-resolution climate data in areas with high spatial climatic variance. This is because neighboring fine-resolution landscape cells with very different climate values are aggregated to their mean in the coarse-resolution climate data, which can reduce the variance among coarse-resolution landscape cells (Woodcock & Strahler, 1987). However, spatial climatic variance may not be underestimated using coarse-resolution climate data in areas with low spatial climatic variance because

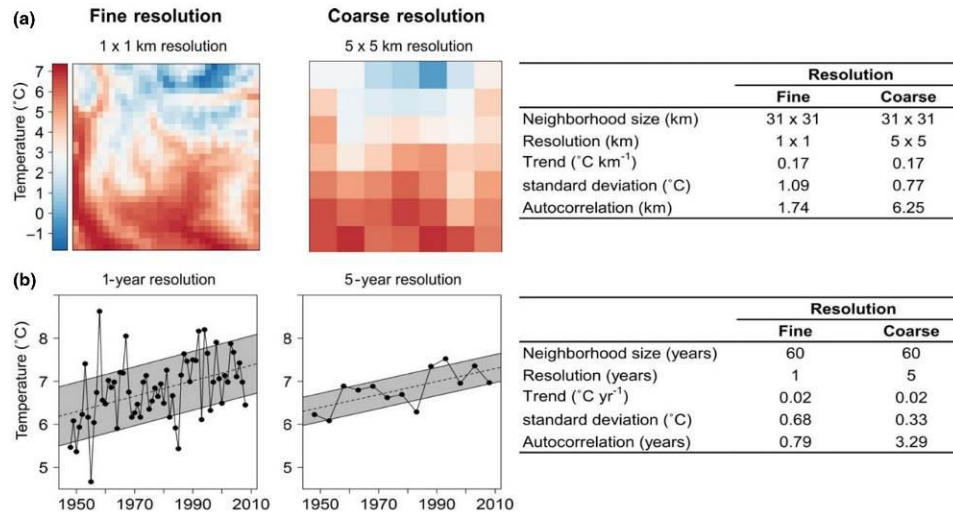
Box 2 An Example of the Effects of Resolution on Climate Data

Fig. B2 One example of how (a) spatial and (b) temporal resolution can affect estimates of trend, variance, and autocorrelation.

Figure B2 provides one example of how using coarse-resolution climate data can affect how trend, variance, and autocorrelation are represented in climate data. Both the spatial and temporal examples are from the same location in the Cascade Mountains of Washington State, United States (latitude = 47.3644, longitude = -120.9110). We scaled the fine-resolution spatial example to a 1 by 1 km resolution and a spatial neighborhood that includes 15 landscape cells in each cardinal direction from the center cell. We scaled the fine-resolution temporal example to a resolution of one year and a temporal neighborhood of 60 years. We created the coarse-resolution examples by increasing the resolution of the climate data by fivefold. The 'coarse' resolution in these examples is still very fine relative to the resolution of climate data used in many climate change impact assessments (Fig. 1). However, this small increase in resolution still affects how trend, variance, and autocorrelation are represented in the climate data. In both the spatial and temporal examples, increasing the resolution did not affect the trend; however, it caused a decrease in the variance and an increase in the autocorrelation (Fig. B2).

the fine-resolution landscape cells have similar climate values to the mean in the coarse-resolution cells (Woodcock & Strahler, 1987).

The magnitude of each climate component varies across the global land surface. Here, we first define and map global climate regimes using the magnitude of each climate component (trend, variance, and autocorrelation) and then evaluate the degree to which using coarse-resolution climate data might misrepresent each climate component in each climate regime.

Methods

We mapped eight different combinations of high and low values of trend, variance, and autocorrelation in mean annual temperature across the global land surface

(Fig. 4). We estimated each of the three climate components using generalized least squares (Appendix S1).

We estimated spatial trend, variance, and autocorrelation by first dividing the global land surface into 31 by 31 km spatial neighborhoods (Box 2). We chose this neighborhood size as a compromise between the size of the neighborhood and the computation time required to estimate each climate component in the neighborhood. We estimated the spatial trend, variance, and autocorrelation within each neighborhood using estimates of historical annual average temperature mapped at a 1 km by 1 km cell resolution (Hijmans *et al.*, 2005). This resolution is similar to the area that encompasses a population for many herpetofauna, plants, and small mammals (Fig. 1) and is the finest spatial resolution of climate data currently available at

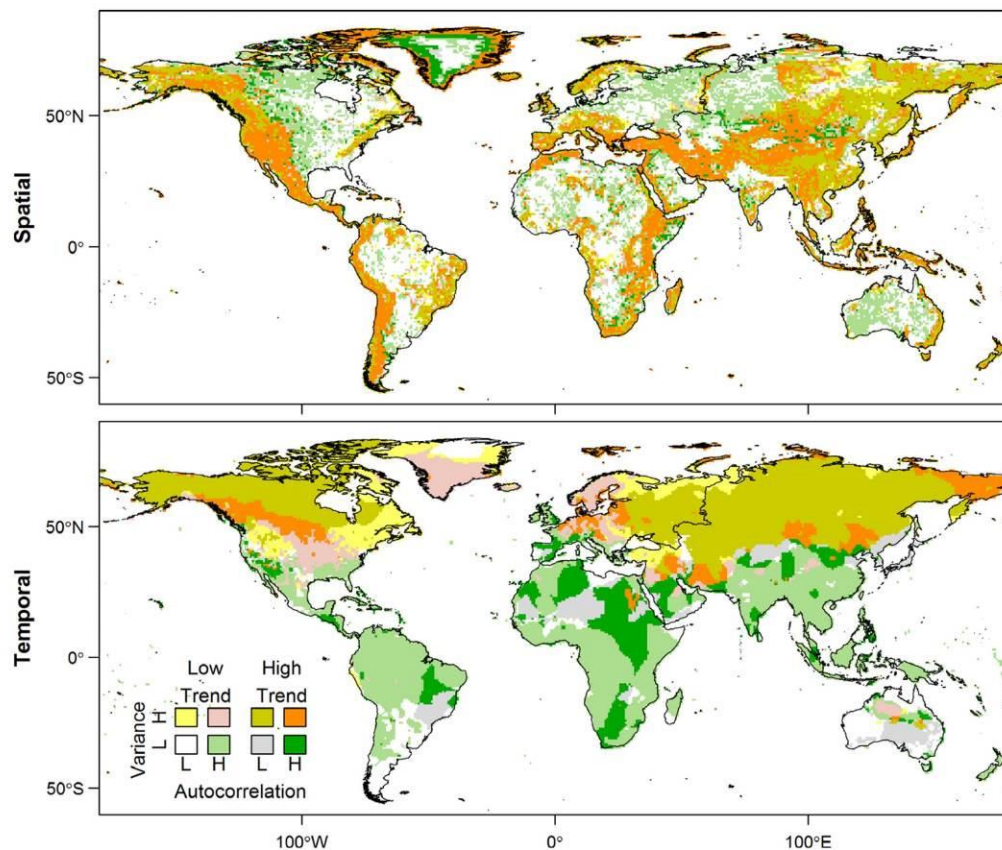


Fig. 4 The location of different climate regimes based on spatial (upper subpanel) and temporal (lower subpanel) climatic variation. The climate regimes are defined using different combinations of high (H) and low (L) values of climatic trend, variance, and autocorrelation in mean annual temperature. Geographical patterns in the spatial climate regimes are robust to our choice of climate data (Fig. S1).

a global scale. This dataset is highly interpolated (Hijmans *et al.*, 2005), which could affect estimates of each climate component. However, we observed little difference between a map of climate regimes generated with this climate dataset and a climate dataset produced with a more mechanistic interpolation procedure (Daly *et al.*, 2002), suggesting that our choice of climate data had minimal effect on our results (Fig. S1).

We estimated temporal trend, variance, and autocorrelation using a time series of annual average temperature between 1900 and 2010 in each 0.5° by 0.5° grid cell covering the global lands surface (Harris *et al.*, 2014).

In both the spatial and temporal cases, we reclassified estimates of trend, variance, and autocorrelation into categorical high and low values using the median value

as the cutoff between high and low. We then mapped different combinations of the high and low values for each climate component to produce maps of eight different global climate regimes for both space and time (Fig. 4). For example, a climate with high spatial trend, low spatial variance, and high spatial autocorrelation was one of the eight climate regimes (Fig. 4).

We chose 1000 random locations in each climate regime and estimated the trend, variance, and autocorrelation at each location using two resolutions. In the spatial context, we used a 1 by 1 km resolution and a 5 by 5 km resolution (Box 2). In the temporal context, we used we used a 1-year resolution and a 5-year resolution (Box 2). We could not use coarser resolutions because decreasing the resolution also

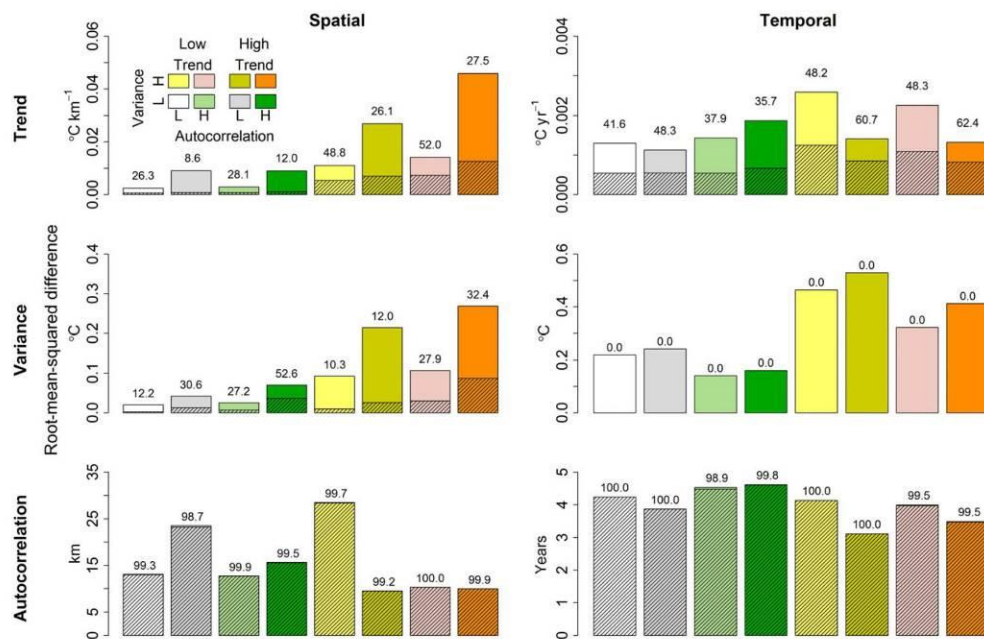


Fig. 5 The effect of using coarse-resolution climate data on estimates of climatic trend, variance, and autocorrelation. Colored bars represent different climate regimes based on combinations of high (H) and low (L) values of each climate component. The locations of these climate regimes are mapped in Fig. 4. Each bar represents the root-mean-squared difference between estimates of the climate component using fine- and coarse-resolution climate data. The hatching and number above each bar represent the proportion of estimates that were positively biased when using coarse-resolution climate data.

decreases the sample size and estimates of trend, variance, and autocorrelation are inefficient with a small sample size.

We evaluated the root-mean-squared difference between estimates of each climate component made using the original resolution and those made using the coarser resolutions. Climate regimes with the highest root-mean-squared difference for each component are the climate regimes where using coarse-resolution climate data has the largest effect on estimates of each climate component. We also evaluated the proportion of the 1000 locations that overestimated the magnitude of each climate component, which provides an assessment of the bias in each climate component caused by using coarse-resolution climate data in each climate regime.

Spatial results

Using coarse-resolution climate data had the largest effect on estimates of spatial trend and variance in

climate regimes with high spatial trend and variance (Fig. 5). Spatial trend and variance were underestimated when using coarse-resolution climate data in most climate regimes. In contrast, coarse climate data overestimated spatial autocorrelation in all climate regimes (Fig. 5). This overestimation was particularly high in two climate regimes: (i) low trend, high variance, and low autocorrelation; and (ii) high trend, low variance, and low autocorrelation.

Temporal results

The effect of using coarse-resolution climate data on temporal trend was largest in climate regimes with low temporal trend and high temporal variance (Fig. 5). Using coarse-resolution climate data had the largest effect on temporal variance in climate regimes with high temporal variance and low temporal autocorrelation and the smallest effect in climate regimes with low temporal variance. Temporal variance was underestimated in all climate regimes when using coarse-resolution climate

data. Temporal autocorrelation was overestimated by a similar amount in all climate regimes when using coarse-resolution climate data.

Where and how could impact assessments be affected

The above results suggest that using climate data with a coarse spatial resolution could have the largest effect on the results of climate change impact assessments in climate regimes with high spatial trend and high spatial variance (Fig. 5). These climate regimes are common in mountainous areas around the globe such as western North and South America (Fig. 4). Climate change impact assessments in these climate regimes could overestimate the rate at which species will need to move to track suitable climates by underestimating the spatial trend (Loarie *et al.*, 2009). They could also overestimate local extinction risk by underestimating the spatial climatic variance, which could underestimate the number of potential climate refugia (Randin *et al.*, 2009; Gillingham *et al.*, 2012; Lenoir *et al.*, 2013). Indeed, estimates of population persistence of high-elevation plants were most affected using coarse-resolution climate data in areas with high spatial variance in temperature (Randin *et al.*, 2009).

Using climate data with a coarse spatial resolution could have the smallest effect in climate regimes with low spatial trend and low spatial variance. These climate regimes are common in flat regions around the globe such as the Great Plains of North America and the Pampas region of South America (Fig. 4).

Using climate data with a coarse temporal resolution could have the largest effect on climate change impact assessments in climate regimes with high temporal variance. Climates with high temporal variance occur in the northern half of the northern hemisphere (Fig. 4). Climate change impact assessments in these areas could overestimate the rate of evolution (Lynch & Lande, 1993; Burger & Lynch, 1995) or the ability of species to shift their ranges under climate change (Canning-Clode *et al.*, 2011; Early & Sax, 2011) by underestimating the temporal variance in climate.

Conclusion

A rich literature exists on the effects of environmental trend, variance, and autocorrelation on population dynamics, adaptation, and extinction risk. However, our review suggests that these components of climate are being misrepresented in many climate change impact assessments because most studies use climate data with a coarse spatial and temporal resolution. Using coarse-resolution climate data, climate change

impact assessments are estimating species responses to climate change on coarse scales that do not accurately capture their exposure to important components of climate. This issue is especially problematic for the majority of organisms on earth that have short dispersal distances like we showed for many reptiles, amphibians, and plants.

Climate data are currently available with a fine temporal resolution (e.g., hourly), and we recommend that climate change impact assessments begin to incorporate climate data with temporal resolutions at least as fine as the generation time of the focal species. However, climate data with an appropriate spatial resolution are unavailable for the vast majority of species with short dispersal distances. Using coarse-resolution climate data may not be as problematic in all areas of the globe. We offer some guidance on where using coarse climate data may have minimal effect on climate change impact assessments and where researchers should use caution. We focused on average annual temperature with a 1 km by 1 km or annual resolution, but our framework could also be applied to other weather variables and other resolutions. For example, daily and seasonal variation can be important to the evolution of species traits (Chan *et al.*, 2016).

We have provided guidance on where using coarse climate data is likely to have the biggest effect on climate change impact assessments based on properties of the regional climate. More research is needed to determine how to choose the appropriate resolution of climate data to match the traits of the focal species and the type of climate change impact assessment being employed. It is unlikely that there is a single resolution that will be appropriate for any given species. Moreover, it is unlikely that downscaling methods will allow for the accurate downscaling of climate data to scales necessary for detailed physiological models (Potter *et al.*, 2013; Bennie *et al.*, 2014). However, research to understand how coarse-resolution climate data will affect climate change impact assessments, and for what species, helps to identify key uncertainties and ensure that policy decisions are based on defensible models.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Estimating climatic trend, variance, and autocorrelation: a file describing how we estimated climatic trend, variance, and autocorrelation in both time and space and whether our choice of climate data affected the results.

Figure S1. The location of different climate regimes in Oregon and Washington USA mapped using different climate datasets (WorldClim and PRISM 800 m data) and the difference between the two maps.

SUPPORTING INFORMATION

Estimating Climatic Trend, Variance, and Autocorrelation:

There are many methods available to estimate trend, variance, and autocorrelation in both space and time. Generalized least squares (GLS) is one method that allows all three climate components to be estimated simultaneously. GLS is a method for estimating the coefficients in a linear regression that can incorporate autocorrelation into the error term. A variogram can be used to estimate the autocorrelation in both the temporal and spatial context. A variogram estimates the degree of covariance between data points separated by different amounts of time or space. The parameters of a GLS model can be estimated with the ‘gls’ function in the ‘nlme’ package in R.

In the temporal context the GLS model can be fit with the focal weather variable as the response variable and time as the independent variable. The coefficient describing the slope between time and the focal weather variable is a measure of the temporal trend. The range of the variogram model measures the time over which the weather variable is autocorrelated. The standard deviation of the residuals from the GLS model measures the temporal variance. Note, that climate data for species with short generation times (i.e., < 1 year) may have a seasonal signal that will need to be accounted for. In this case, the autocorrelation and variance can be estimated with a seasonal autoregressive integrated moving average (ARIMA) model and the trend can be estimated using a linear regression of the residuals from the ARIMA model.

In the spatial context, the GLS model can be fit with the focal weather variable as the response variable and the x and y spatial coordinates as the independent variables. The spatial trend can be estimated as a combination of the trend in the x and y directions:

$$\beta = \sqrt{\beta_x^2 + \beta_y^2},$$

where β is the average maximum slope, and β_x and β_y are slopes in the x- and y- directions (respectively). The variance and autocorrelation are estimated using the range of the variogram model and the standard deviation of the residuals, as in the temporal case. In the spatial context, the range of the variogram model measures the distance over which the weather variable is autocorrelated.

Does the choice of Spatial climate data affect the climate regime maps?

The spatial climate data we used to define and map spatial climate regimes (WorldClim, Hijmans et al. 2005) is highly interpolated, which could affect our results by affecting estimates of each climate component. To address whether our choice of highly interpolated climate data affected our definition of different climate regimes, we evaluated whether climate regimes were classified the same in Oregon and Washington states when analysis was conducted using WorldClim and PRISM 800 m climate data. Although these datasets are both interpolated datasets with a similar resolution, spatial variation in climate is known to differ between these datasets in Oregon and Washington due to differences in the interpolation procedure (Hijmans et al. 2005). The WorldClim dataset is based on a simple interpolation procedure that uses data from weather stations along with latitude, longitude, and elevation to estimate temperature in each cell of the landscape (Hijmans et al. 2005). PRISM uses a much more mechanistic algorithm that accounts for the effects of longitude, latitude, elevation, topographic facets (e.g., leeward and windward sides of mountains, north- and south-facing slopes), coastal effects, multiple atmosphere layers, and the position and form of mountain ranges (Daly et al. 2002). The PRISM algorithm also incorporates expert knowledge to control the local weighting of each climate driver in the interpolation procedure. Consequently, PRISM climate data produces a

much more detailed picture of climate in topographically diverse areas with few weather stations such as Oregon and Washington states.

We used the same procedure described in the paper to map climate regimes using both datasets. We used the same values as we used for our global analysis (i.e., the global median) to separate low and high values of trend, variance, and autocorrelation for both datasets. We then compared the maps to determine the proportion of cells that were given the same classification between the two datasets. If using WorldClim data affected our results we would expect a high proportion of cells to be classified differently among the two datasets.

Despite major differences between the two climate datasets, geographic patterns in the climate regimes in Oregon and Washington were similar between maps produced using the two datasets. Seventy-two percent of cells have the same classification between maps produced with the two datasets. These results suggest that the climate regime maps in Fig. 4 are robust to our choice of climate data.

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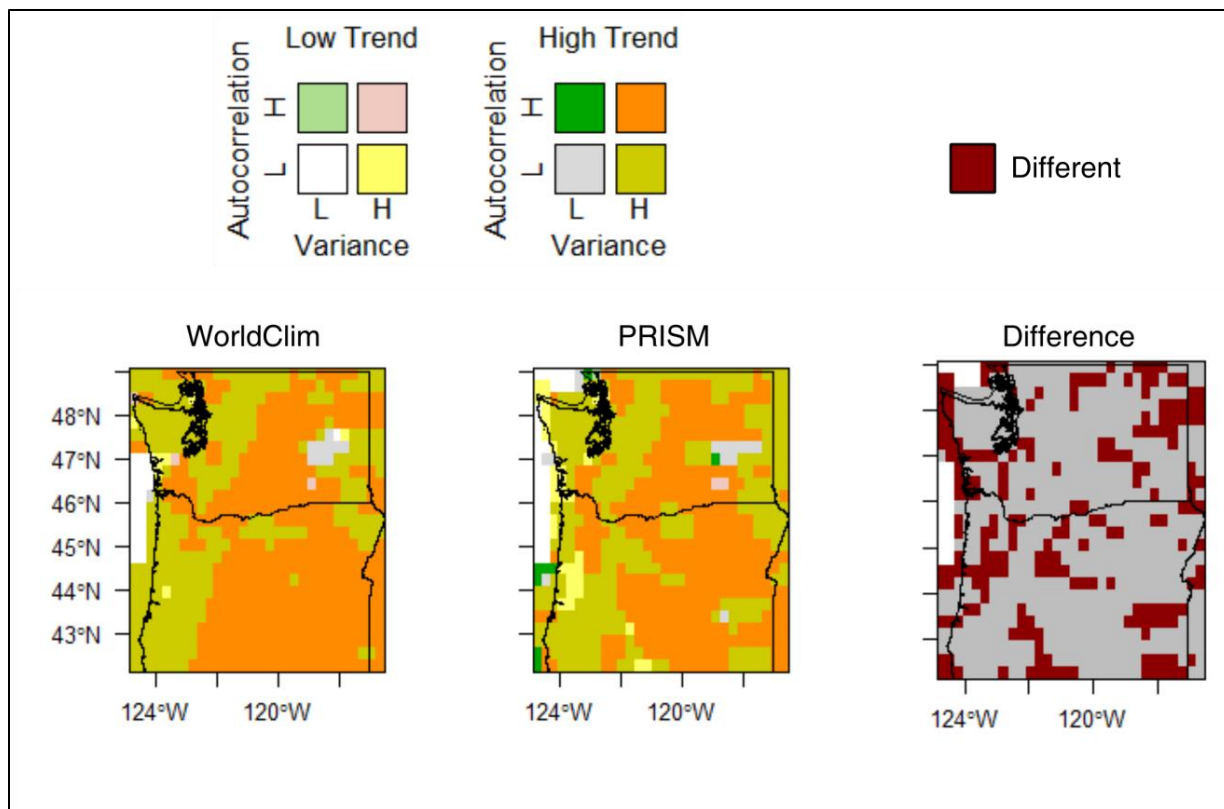


Figure S1. The location of different climate regimes in Oregon and Washington USA mapped using different climate datasets (WorldClim and PRISM 800m data) and the difference between the two maps. The climate regimes are based on different combinations of high (H) and low (L) values of spatial climatic trend, variance, and autocorrelation in mean annual temperature. The maps show similar geographical patterns; 72% of cells have the same classification between the two maps. The majority of cells (77%) with a different classification have different estimates of autocorrelation. These results suggest that the climate regime maps in Fig. 4 are robust to our choice of climate data.

Chapter 2: Climates Past, Present, and Yet-to-Come Shape Climate Change Vulnerabilities



Climates Past, Present, and Yet-to-Come Shape Climate Change Vulnerabilities

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Review

Climates Past, Present, and Yet-to-Come Shape Climate Change Vulnerabilities

Christopher P. Nadeau,^{1,*} Mark C. Urban,^{1,2} and Jon R. Bridle³

Climate change is altering life at multiple scales, from genes to ecosystems. Predicting the vulnerability of populations to climate change is crucial to mitigate negative impacts. We suggest that regional patterns of spatial and temporal climatic variation scaled to the traits of an organism can predict where and why populations are most vulnerable to climate change. Specifically, historical climatic variation affects the sensitivity and response capacity of populations to climate change by shaping traits and the genetic variation in those traits. Present and future climatic variation can affect both climate change exposure and population responses. We provide seven predictions for how climatic variation might affect the vulnerability of populations to climate change and suggest key directions for future research.

Climatic Variation and Vulnerability

Climate change is altering all aspects of biological systems, from genes to ecosystems [1]. By 2100, climate change could cause the extinction of one in six species, alter the abundance and distribution of many that remain, and generate novel ecological communities [2,3]. These changes will fundamentally alter life and have large impacts on human wellbeing [4]. Identifying which populations will be most **vulnerable** (see [Glossary](#)) to climate change has therefore become a major focus of ecology and evolutionary biology.

Climate change vulnerability depends on a population's **exposure** to climate change, **sensitivity** to abiotic and biotic changes, and its ability to respond to those changes (i.e., **response capacity**) (Figure 1) [5,6]. The response capacity of a population depends on factors such as dispersal ability and genetic variation in traits affecting fitness (**intrinsic response capacity**) as well as on environmental factors such as dispersal barriers that influence climate change responses (**extrinsic response capacity**) [5,6].

We present a framework outlining how spatial and temporal variation in climate and weather are key factors affecting each of these vulnerability components (Figure 1). We follow previous research that defines temporal variation in relation to the resolution of an organism's generation time, and spatial variation in relation to the resolution of the area inhabited by a population (Box 1) [7,8]. Defining temporal and spatial climatic variation in this way is consistent with the population-level responses that often underlie responses to environmental change, although other resolutions remain important (Box 1; see Outstanding Questions).

We suggest that historical variation in weather and climate has shaped the sensitivity and intrinsic response capacity of different populations and species to climate change by driving

Trends

Predicting the vulnerability of populations to climate change is crucial.

Spatial and temporal climatic variation strongly influence vulnerability.

Historical climatic variation can shape traits that affect vulnerability.

Present and future climatic variation affect exposure and population responses.

Maps of climatic variability can predict where populations are most vulnerable.

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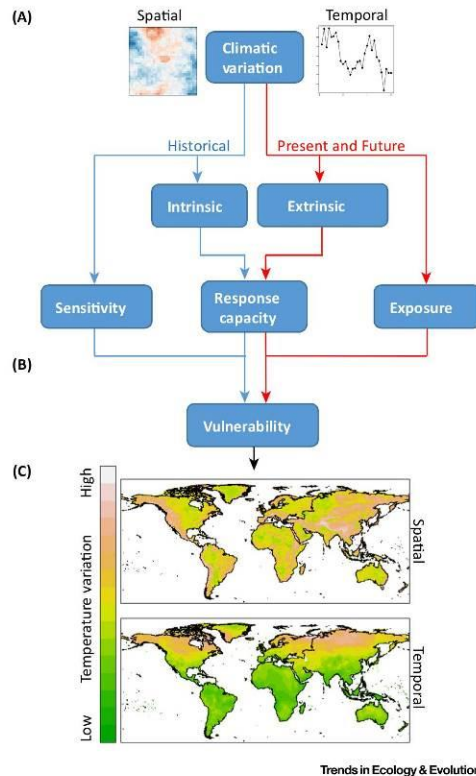


Figure 1. A Conceptual Model of How Spatial and Temporal Climatic Variation Predict the Vulnerability of Populations to Climate Change. (A) Spatial and temporal climatic variation affect the exposure, sensitivity, and response capacity of populations under climate change. Historical climatic variation affects the intrinsic response capacity and sensitivity of populations, and present and future climatic variation affect the exposure and extrinsic response capacity. (B) Exposure, sensitivity, and response capacity are key components determining the vulnerability of populations to climate change. (C) Given that climatic variation differs around the globe, maps of climatic variation scaled to the traits of the focal population (e.g., dispersal ability, generation time; [Box 1](#)) can predict where and why populations will be most vulnerable to climate change. The upper map shows current spatial variation within 31×31 km pixels and was produced using climate data with a 1 km resolution [93]. The lower map shows interannual variation in temperature between 1900 and 2010 based on Climatic Research Unit TS 3.23 data [94].

trait evolution and trait variation within and among populations ([Figure 1](#)). In addition, present and future variation in weather and climate will affect exposure and extrinsic response capacity ([Figure 1](#)). Given that climatic variation differs around the globe, estimating regional climatic variation and interpreting this variation from an organismal perspective ([Box 1](#)) should help to predict where and why populations will be vulnerable to climate change ([Figure 1](#)).

We present seven testable predictions of how the sensitivity and response capacity of populations will differ between regions with high and low spatial or temporal climatic variation ([Figure 2](#)). We then suggest future research directions to test these predictions, and summarize the types of climates where populations are likely to be most at risk from climate change.

Glossary

Additive genetic variation: the portion of phenotypic variance among individuals that is due to the average effects of alleles across many genotypes and not due to dominance or epistasis. Additive genetic variation determines the potential for evolutionary responses.

Exposure: the amount of climate change experienced by an individual or population in the absence of any response (e.g., movements, changes in phenology) to that change [5].

Extrinsic response capacity: the component of response capacity determined by factors external to an individual or population [5]. These factors constrain the intrinsic response capacity during the response. For example, dispersal barriers can limit the ability of a population to track suitable climates, thereby decreasing its extrinsic response capacity.

Intrinsic response capacity: the component of response capacity determined by individual and population-level traits (e.g., dispersal ability, genetic variation in phenology). For example, a population with high dispersal propensity will be better able to track suitable climates and will therefore have a higher intrinsic response capacity.

Microrefugia: small areas relative to the traits of the focal species or population where microclimates or microclimate variation buffers populations against climate change [64].

Phenotypic plasticity: the degree to which a single genotype expresses different phenotypes in response to changes in the environment. Phenotypic changes can occur in the lifetime of an individual (i.e., reversible plasticity) or be fixed during development (i.e., irreversible plasticity).

Response capacity: the ability of an organism, population, or species to mitigate the adverse effects of climate change [5] by tracking suitable habitats, evolutionary adaptation, or phenotypic plasticity. Response capacity is commonly referred to as adaptive capacity [5], but we use here the term response capacity to reduce confusion with the narrower evolutionary definition of adaptive capacity. Response capacity can be partitioned into two

The Ghosts of Climate Past

Prediction 1: Populations from Climates with High Temporal or Spatial Variation Will Maintain Higher Genetic Diversity Which Increases Their Intrinsic Response Capacity

If an environment varies in time or space, different genotypes can be favored at different times or locations. This varying selection can maintain high genetic variation in fitness despite stabilizing selection acting to reduce genetic variation [9]. Populations from climates with historically high temporal or spatial variation could therefore maintain higher **additive genetic variation** in fitness that allows them to evolve adaptations to climate change, increasing their intrinsic response capacity (Figure 2A).

Temporal environmental variation that occurs among generations can preserve genetic variation by favoring different traits at different times and preventing one genotype from dominating a population [10–12]. This process can be enhanced for long-lived species or species with propagule banks because old individuals or propagules can be less affected by episodic natural selection and therefore persist in the population despite many generations experiencing different selective optima [10,11,13]. For example, interannual temperature variation maintains genetic variation in silver birch (*Betula pendula*) stands by favoring the recruitment of different genotypes in different years [10]. This genetic variation could facilitate evolutionary adaptation to climate change over the next 33–55 years [10]. In another example, seasonal temperature variation maintained genetic variation in *Drosophila subobscura* that facilitated a rapid evolutionary response to a recent heat wave [14].

Theory suggests that spatial climatic variation within and among populations can maintain more genetic variation than temporal variation [9] by mixing individuals adapted to different local conditions [15,16]. For instance, genetic variation in lodgepole pine (*Pinus contorta*) is higher in regions with higher spatial climatic variation [17]. This mechanism requires that gene flow is sufficient to spread alleles within and among populations, but not enough to prevent local

components: intrinsic and extrinsic response capacity.

Sensitivity: the degree to which climate change will adversely affect the fitness of an individual or population that does not respond to changing climates [5]. Sensitivity quantifies the fact that the same change in climate will not affect all organisms equally.

Thermal neutral zone: the temperature range within which the rate of heat production by an endotherm is in equilibrium with the rate of heat loss to the environment. Outside this zone an endotherm must expend energy to thermoregulate.

Vulnerability: the propensity to be adversely affected by climate change, including (but not limited to) decreases in abundance, loss of genetic variation, extirpation, and extinction [5]. Vulnerability is often partitioned into three components: exposure, sensitivity, and response capacity.

Box 1. An Organismal Perspective on Climatic Variation

Climates and weather vary on multiple spatial and temporal scales ranging from millimeters and minutes to kilometers and millennia. Organisms experience this variation differently depending on their life history and behaviors. Researchers must consider how the focal organism experiences climatic variation to make accurate predictions of climate change responses. We highlight here three key aspects of this organismal perspective.

Life History and Behavior

Organisms experience climatic variation differently depending on their life history and behavior [59]. For example, a species might have a particularly sensitive life-stage [59,84] or avoid extreme weather through behaviors such as hibernation or by utilizing particular microclimates [57,59]. To accurately predict climate change responses, it is crucial to focus on the most sensitive life-stages, model important behaviors, and filter climate data to include only those time periods when a species is active.

Biological Scaling of Climate Data

Accurately predicting climate change responses requires scaling climate data to the organism and process under investigation [7,96]. Figure 1 shows how scaling of the study area, focal time period, and resolution of climate data might differ between two species with different dispersal abilities and generation times. These scaling differences affect how the organisms experience spatial and temporal climatic variation. For example, the red fox (*Vulpes vulpes*) will experience more spatial climatic variation within the study area (Figure 1A), but cow wheat (*Melampyrum lineare*) will experience greater temporal temperature variation among generations (Figure 1B).

Most climate change impact assessments do not scale climate data based on the biology of focal species [7,89], and this likely reduces predictive accuracy [79,81,91,97]. More research will be necessary to determine how best to scale climate data to accurately represent climatic variation in climate change vulnerability assessments (see Outstanding Questions).

Effects of Different Resolutions

Climatic variation at different resolutions can have opposing effects on the same population. For instance, when temperature varies within generations, populations often evolve narrow thermal tolerances and concentrate their activity during times when temperatures are suitable [47,98]. However, this strategy could be maladaptive when temperatures vary among generations because temperatures might never be suitable during the lifetime of future offspring. Thus, populations evolve broad thermal tolerances to cope with temperatures that vary among generations [47,98]. More research is needed to determine the effect of climatic variation at different resolutions and how variation at different resolutions interacts to affect species traits (see Outstanding Questions).

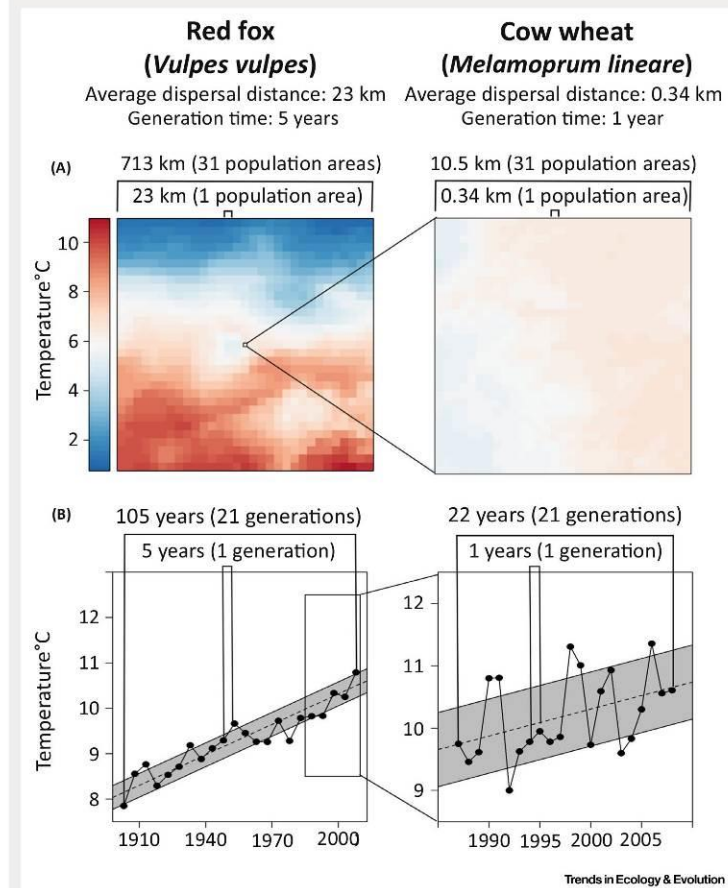
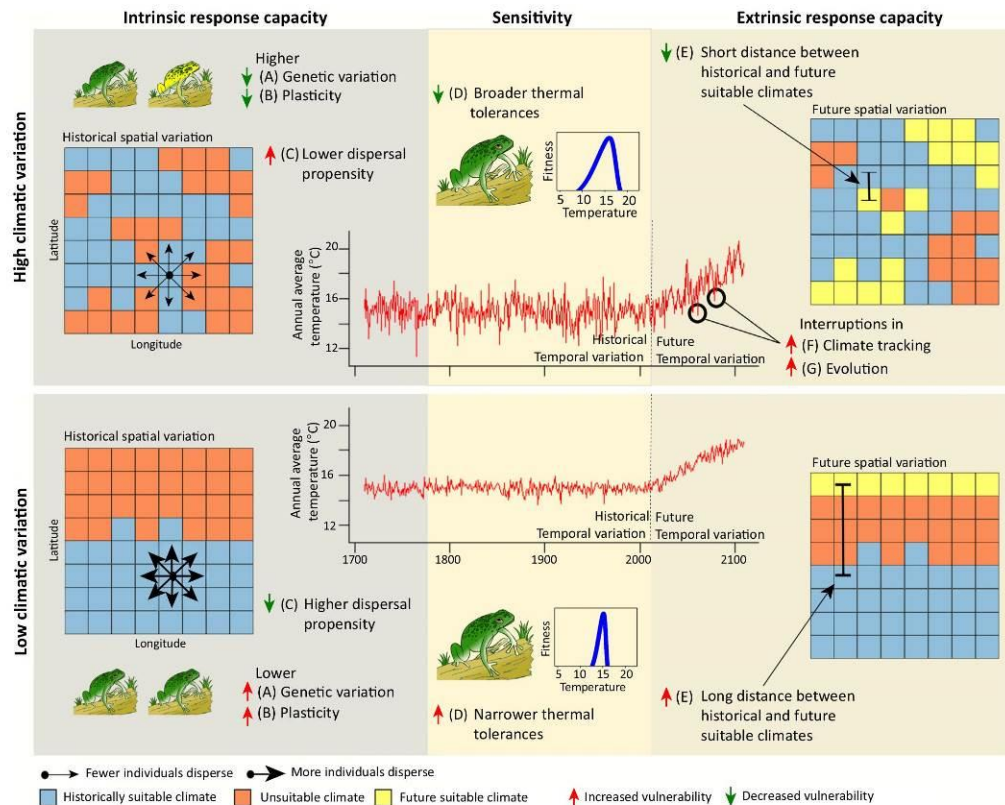


Figure 1. Examples of (A) Spatial and (B) Temporal Climatic Variation for Species with Different Dispersal Abilities and Generation Times. We scaled the spatial resolution (i.e., the grid cell area) to be the area inhabited by a population for each species, which we define as the area encompassing 86.5% of dispersal events (i.e., Wright's dispersal neighborhood [7,15]). We scaled the study area to include 15 population areas in each cardinal direction from the center cell. We scaled the temporal resolution to one generation and the focal time period to include 21 generations. Scaling the study area, focal time period, and resolution of the climate data in this way demonstrates how species with different dispersal abilities and generation times might experience climatic variation differently. The red fox will experience more spatial climatic variation in its study area, but cow wheat will experience more temporal temperature variation among generations in the focal time period. This figure is modified from [7].



Trends in Ecology & Evolution

Figure 2. Seven Potential Differences in the Sensitivity, Intrinsic Response Capacity, and Extrinsic Response Capacity of Populations from Locations with High or Low Spatial and Temporal Climatic Variation. Effects on vulnerability are shown with the colored arrows. Historical spatial and temporal variation can maintain higher (A) genetic variation (Prediction 1) and (B) plasticity (Prediction 2), increasing the intrinsic response capacity of a population. (C) Historical spatial variation can decrease dispersal propensity, decreasing the intrinsic response capacity of a population (Prediction 3). (D) Historical temporal variation can increase thermal tolerance breadth, decreasing the sensitivity of a population (Prediction 4). (E) The distance between current and future suitable climates is shorter in climates with high spatial climatic variation, increasing the extrinsic response capacity of a population (Prediction 5). Present and future temporal variation can cause interruptions in (F) climate-tracking (Prediction 6) and (G) evolution (Prediction 7), decreasing the extrinsic response capacity of a population.

adaptation [17–19]. In addition to increasing additive genetic variation [17], spatial climatic variation can provide a source for individuals pre-adapted to future climates [20,21]. For instance, warm-adapted genotypes might move to higher altitude sites, displacing cold-adapted genotypes as they go [20,21].

Populations that occur in temporally variable climates might not have higher genetic variation if they can avoid local weather extremes, for example by moving among microclimates within an area. Further, genetic variation in small isolated populations, such as those that occur on mountaintops, could remain low despite high temporal and spatial climatic variation [22]. Whether genetic variation will allow populations to evolve sufficiently rapidly to persist under climate change depends on many factors (Prediction 7) [23–25]. Evolution might also be

slowed by **phenotypic plasticity** [26], which can evolve under climatic variation (Prediction 2). Theory suggests, however, that plasticity is more likely to facilitate than hinder evolution under climate change by buffering populations from declines and providing extra time for evolutionary responses [26].

Prediction 2: Populations from Climates with High Temporal Variation Will Have Higher Phenotypic Variation, Thereby Increasing Their Intrinsic Response Capacity

Genotypes within populations often vary their phenotype to cope with high temporal variation in climate that occurs either within or among generations. Two different strategies of phenotypic variation have evolved depending on the predictability of climatic variation (Box 2): phenotypic plasticity and bet-hedging. Both could increase the intrinsic response capacity of a population.

In climates with high temporal variation that is predictable via a cue (e.g., seasonal temperature variation predicted via day length), populations typically evolve adaptive phenotypic plasticity [27,28]. Changes in physiology and the timing of flowering or migration are common examples. If environmental cues remain reliable under climate change, plasticity could increase the intrinsic response capacity of populations by allowing phenotypic adjustments to climate change [26,29]. Indeed, many populations have already adjusted the timing of key events (e.g., migration) and traits (e.g., body size) in response to recent climate change [29]. Such plastic responses might not be enough for population persistence, but could allow time for other climate change responses to become effective (e.g., evolutionary adaptation [30,31]). However, plasticity will only increase the intrinsic response capacity of a population if the cue remains reliable and the phenotype generated under novel climates remains adaptive [26,32].

In climates with high temporal variation that is unpredictable (e.g., interannual rainfall in arid regions; Box 2) populations often evolve diversified bet-hedging strategies where individuals produce offspring with different phenotypes or oviposit in different microclimates to spread their

Box 2. Biological Effects of Climatic Autocorrelation and Predictability

We focus here primarily on the magnitude of climatic variation, contrasting locations with high and low variation (Figure 2). However, the autocorrelation and predictability of climatic variation are also important.

Autocorrelation describes the similarity between neighboring measurements of weather or climate in time or space (Figure 1). If climatic variation is positively autocorrelated, then the conditions in one time period or location will be similar to conditions in neighboring time periods or locations (Figure 1 in Box 1). Positively autocorrelated climates have longer time periods of similar weather or larger areas of similar climate. Climatic variation that is positively autocorrelated is also predictable because the weather or climate in the current time period or location is likely to be similar in neighboring time periods or locations (Figure 1 in Box 1). Climatic variation can also be predictable from external cues such as day length or tidal variation.

Autocorrelation and predictability of historical climatic variation have had strong biological effects. For example, populations evolve phenotypic plasticity when historical weather is predictable because phenotypic adjustments to match the current environmental conditions are likely to be adaptive in future time periods [27,28]. However, if conditions vary unpredictably, then phenotypic adjustments in response to current weather are unlikely to be adaptive under future conditions. Therefore, when weather varies unpredictably, populations evolve bet-hedging strategies such as variation in the duration of dormancy in seed banks of desert plants [27,28,33,34]. The autocorrelation of historical climatic variation can also affect the evolution of dispersal propensity (Prediction 3).

The effect of autocorrelation in current and future climatic variation has received less attention, but is likely to be an important factor in predicting climate change responses. For example, one of the few studies that focused on current temporal autocorrelation demonstrated how sustained warm periods in a climate that is temporally autocorrelated can allow a warm-adapted species to shift its distribution under climate change by providing a sustained competitive advantage over resident species [99]. Temporal autocorrelation can also affect evolution to changing climates by affecting the rate of evolution (Prediction 7) and the fate of beneficial mutations [100]. Presumably, spatial

autocorrelation will also affect the ability of species to track suitable climates by affecting the size of climatically suitable patches and the size of climatic dispersal barriers [35,79]. Such effects of spatial autocorrelation on the responses of species to climate change require more detailed research.

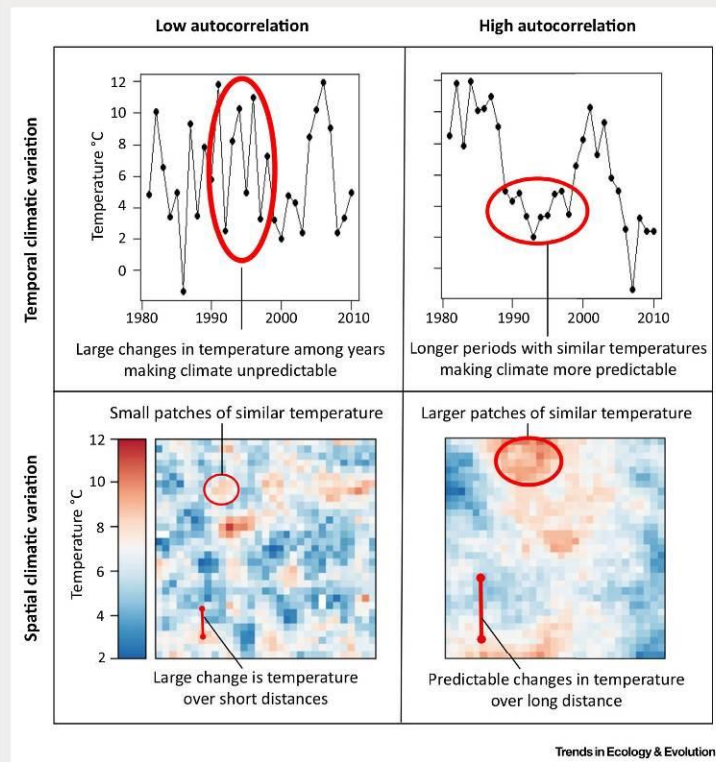


Figure 1. Examples of Spatial and Temporal Climatic Variation with Different Amounts of Autocorrelation. Climatic variation with higher autocorrelation has longer time periods or larger distances with similar climates, and this makes climate more predictable over time and space.

risk in unknown future conditions [27,28,33]. These strategies reduce the long-term variance in fitness, and this increases population persistence in a variable environment even though population mean fitness might be reduced. Bet-hedging could increase the intrinsic response capacity of a population by reducing the fitness costs of unfavorable future conditions and allowing time for other climate change responses such as climate-tracking and evolution. Bet-hedging is likely to be especially effective in the short-term when environments vary between novel and historical conditions. However, bet-hedging will only increase the intrinsic response capacity if the costs (e.g., seed bank mortality) remain sufficiently low under future climates [34].

Prediction 3: Populations from Climates with Low Spatial or High Temporal Variation Will Evolve Higher Dispersal Propensity Which Increases Their Intrinsic Response Capacity
Dispersal is risky in spatially variable climates with low autocorrelation (Box 2) because a disperser is likely to encounter unsuitable climates (Figure 2C) [35,36]. Remaining in a location with unpredictable temporal variation (Box 2) is also risky because the current location could become unsuitable in the future [36,37]. Consequently, populations from locations with low spatial climatic variation or high temporal climatic variation often evolve higher dispersal propensity [36–38].

Higher dispersal propensity can allow populations to track suitable climates under climate change. For example, European dragonflies from standing freshwater systems have higher dispersal propensity than those from running freshwater systems because standing systems are more ephemeral on long-time scales, although other explanations exist [39]. The higher dispersal propensity of dragonflies from standing systems allowed them to recolonize central Europe after the last glaciation [39], occupy a greater portion of suitable habitat [40], and track contemporary climate change better than species from running systems [41].

The evolution of dispersal propensity depends on many other factors such as the need to avoid inbreeding or competition [37]. However, spatial and temporal environmental variation is a key factor that could predict the dispersal propensity [37] and therefore the intrinsic response capacity of many populations.

Prediction 4: Populations from Climates with High Temporal Variation among Generations Will Evolve Broad Thermal Tolerances That Decrease Their Sensitivity to Climate Change
Seventy years ago, Scholander *et al.* observed that endotherms have a broader **thermal neutral zone** in the arctic than the tropics [42]. Two decades later, Janzen suggested that temperate ectotherms evolved broader thermal tolerances than tropical ectotherms in response to greater temperature seasonality in temperate regions [43]. Recent studies confirm these patterns [44,45] and demonstrate a clear link between thermal tolerance breadth and seasonal temperature variation (Boxes 1 and 3) [46,47].

Evolved differences in thermal neutral zones and tolerances due to seasonal temperature variation (Box 3) strongly affect climate change sensitivity (Figure 2D) [44,48–50]. Populations with broader thermal tolerances are less likely to experience heat stress under climate change [44,48,50]. Moreover, species with broader thermal tolerances often have larger geographical ranges [47,51], and this can reduce their vulnerability to climate change because their range is

Box 3. Temperature Variation and Climate Change Sensitivity

Organisms from climates with higher temperature seasonality often have broader thermal tolerances [42–45], but do not necessarily have higher thermal maxima (*cf* upper limits in Figure I). In fact, upper thermal tolerances vary little within and among species across broad temperature gradients [45]. Why then might organisms from climates with high temperature seasonality be less sensitive to climate change?

The answer is due, in part, to the commonly observed steep decline in fitness at warmer temperatures, which makes it costly to experience temperatures warmer than the optimum (Figure I). Under variable temperatures, an organism maximizes long-term fitness by living in a location that is cooler on average than the optimal temperature (Figure I). This reduces the likelihood of experiencing temperatures warmer than the optimum, which would cause severe fitness declines (Figure I). As temperature variation increases, the difference between the average temperature where an organism occurs and the optimal temperature (i.e., thermal safety margin) [48] also increases. Large thermal safety margins can buffer increases in average temperature due to climate change by decreasing climate change sensitivity (Figure I) [48].

In addition, organisms in cooler climates often have an increased buffering capacity because there is a bigger difference between the average environmental temperature where they occur and their upper thermal tolerance limit (i.e., warming tolerance; Figure I) [48]. Climates with high temporal temperature variation often occur at northern latitudes where average temperatures are also cooler. Consequently, organisms in cool, variable climates also tend to have a greater warming tolerance (Figure I) [48]. This additional buffering capacity in climates with high temperature seasonality further decreases climate change sensitivity [48].

Lastly, organisms in locations with higher temperature seasonality can often shift their phenology to cope with increasing temperatures. Indeed, the projected vulnerability of temperate organisms to climate change decreased substantially when models allowed for phenological responses to climate change [48,58]. In fact, increasing temperatures will lengthen the active season for many ectotherms living in cooler climates, and this could increase long-term fitness [48,58]. By contrast, phenological shifts are less likely to help populations in locations with little temperature seasonality because shifts in activity time will not correspond to large temperature changes.

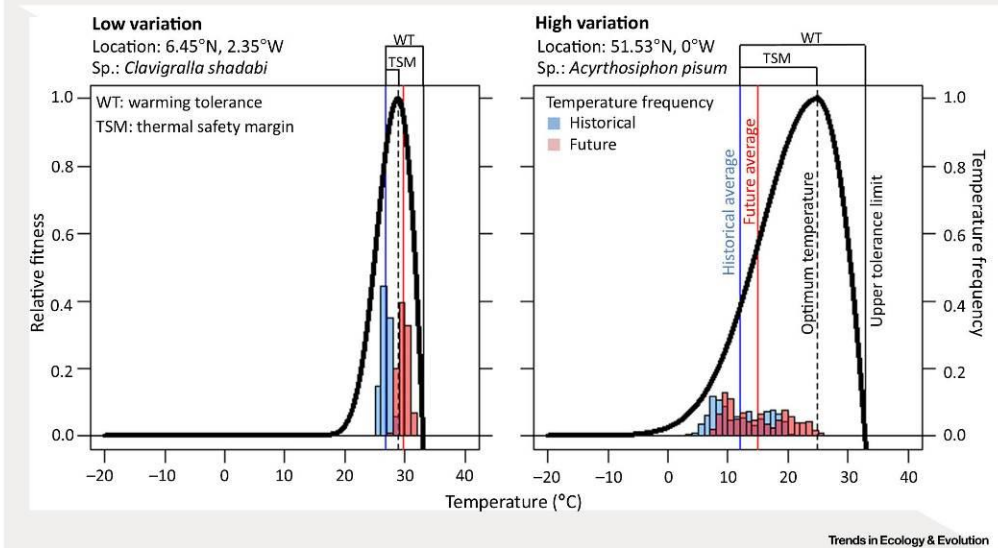


Figure 1. Thermal Performance Curves (Thick Black Line) from Two True Bug (Hemiptera) Populations That Occur in Climates with Low (Left) and High (Right) Temporal Variation in Temperature. Historical (blue), future (red), and overlapping (purple) temperature variation is shown in the histograms, and averages are shown by the colored vertical lines. The optimal temperature is shown by the dashed line and the upper tolerance limit is shown by the thin black line. The current thermal safety margin (TSM) and warming tolerance (WT) are shown above each plot. Populations from more variable climates have larger thermal safety margins and warming tolerances, which makes them less sensitive to climate change. Temperature data were obtained from the National Center for Atmospheric Research model [95] forced under Resource Concentration Pathway 8.5. This figure is modified from [48].

more likely to incorporate low vulnerability regions (e.g., low exposure, fewer dispersal barriers) [52,53]. Therefore, temperate organisms are often predicted to be less vulnerable to climate change than tropical organisms, despite higher predicted increases in temperature in temperate versus tropical regions [44,48,54].

These predictions depend on a few key assumptions [55–57]. Predictive models must represent future temperature variation accurately, convert environmental temperature to body temperature, and allow for negative intrinsic population growth rates to make accurate future predictions of vulnerability [49,50,55,57–59]. Models with these assumptions often predict that species in the subtropics are most vulnerable to climate change because they live closer to their upper thermal limit (Box 3), but experience relatively high temperature variation [50,58]. Nevertheless, fitness losses in the subtropics could be moderated by lengthening growing seasons [58]. In addition, fitness measured at constant temperatures or for short periods, as is customary when measuring thermal tolerances, might not predict fitness under variable temperatures or under prolonged exposure [60,61]. Organisms might also regulate their temperature behaviorally (e.g., by moving among microclimates), and this would limit their

vulnerability to climate change [55,57,62]. However, these behaviors often come with high costs, such as reduced foraging time, which can negate their benefits [63]. Despite these caveats, the relationship between temporal temperature variation and thermal tolerances should indicate which populations are most sensitive to climate change.

Extrinsic Response Capacity under Climates Present and Yet-to-Come

Prediction 5: Climate-Tracking Will Be More Effective in Climates with High Spatial Variation, Which Increases the Extrinsic Response Capacity of Populations

Climate can differ dramatically over short distances owing to factors such as topography, shading, and proximity to large water bodies [64]. For example, temperature differences over a few meters in a forest canopy can mimic those observed over hundreds of meters in elevation or many kilometers in latitude [38]. In contrast, climates might be similar across hundreds of meters in other landscapes.

Spatial climatic variation will affect the extrinsic response capacity of a population by affecting how populations track suitable climates. Populations in locations with little variation will often need to move long distances to track suitable climates (Figure 2E), making them more vulnerable to climate change [65]. Conversely, high spatial climatic variation could facilitate climate-tracking in several ways. Populations might only need to move short distances to track suitable climates or avoid extreme weather events (Figure 2E) [65,66]. Patches of suitable climate could also act as stepping stones through unsuitable areas or **microrefugia** where populations could persist for many decades [64,67,68]. Many populations are thought to have persisted in such microrefugia throughout past climate changes [69–71], and many studies suggest that microrefugia will be crucial for population persistence under future climate change [72–74].

High spatial climatic variation can also allow small populations to persist outside the more contiguous parts of a species range. These populations can expand when the surrounding climate becomes suitable, increasing range expansion rates from those predicted based on homogeneous environments [71,75,76]. This mode of climate-tracking could explain how trees quickly refilled their ranges during post-glacial climate warming in North America and Europe [71,75].

Spatial variation might also hinder climate-tracking under some circumstances. Unsuitable climates can act as dispersal barriers, especially for species with narrow climatic tolerances [43,77]. High spatial climatic variation can also increase the likelihood that passive dispersers settle in unsuitable locations [35].

Prediction 6: Populations Will Track Suitable Climates More Slowly in Climates with High Temporal Variation, and This Decreases Their Extrinsic Response Capacity

In climates with high temporal variation, weather during a relatively short period (e.g., days, weeks, decades) can differ substantially from the long-term trend. For example, February 2015 in the northeastern USA was the second coldest on record despite a 3.9 °C increase in average February temperature since 1900 [78].

Periods that deviate from the long-term trend can slow climate-tracking if climates along range-shift pathways become temporarily unsuitable [76,79–81] or by eliminating populations that colonized regions that recently became suitable (Figure 2F) [82–84]. For example, amphibians in the western USA might not track suitable climates because decadal climate fluctuations cause gaps between areas where climate is currently suitable and areas predicted to be suitable in the future [79]. In addition, a short cold snap in winter 2010 led to range retractions of exotic species that had previously expanded their range from the Caribbean into the USA [82].

Decreased climate-tracking rates can increase extinction risk under climate change [79,81], especially for populations and life-stages that are sensitive to short-term climate fluctuations [79,84].

Prediction 7: Evolutionary Adaptation of Populations Will Lag Further behind Long-Term Climate Change in Regions with High Temporal Variation, Thereby Decreasing the Extrinsic Response Capacity of Populations

Theoretically, a population can evolve adaptations in response to current and future climate change provided that the rate of climate change does not exceed a critical rate, which depends on generation time, maximum population growth rate, genetic variation in fitness, and the strength of selection [24,25]. However, current and future temporal environmental variation among generations can reduce the rate of climate change to which a population can adapt, decreasing the extrinsic response capacity of a population (Figure 2G).

Temporal climatic variation among generations can cause adaptations to climate in one time period to be maladaptive in subsequent time periods as the environment varies [24]. This maladaptation can cause demographic and genetic bottlenecks that slow adaptation rates by removing standing genetic variation [24]. The rate of environmental change a population can adapt to is less affected if temporal variation is autocorrelated (Box 2) because evolution in one time period is less likely to be maladaptive in subsequent time periods [85]. Recent predictions of the evolution of wing melanin in alpine and subalpine butterflies demonstrate how temporal variation in weather can slow evolutionary adaptation to climate change [86]. In this example, temperature variation caused variation in the direction (for or against wing melanin) and the magnitude of selection, resulting in very little directional evolution under recent climate change despite directional changes in temperature.

Under some circumstances, however, high climatic variation can aid evolutionary adaptation. For instance, extreme weather events can remove maladapted adults of long-lived organisms, and this can facilitate the recruitment of better-adapted individuals [87].

Testing Predictions Is the Next Step

Many studies forecast climate change responses for particular populations or regions, but rarely test their predictions using data from the responses of populations to recent climate change or climate change experiments. An important next step is to test the predictions presented here using climate change experiments and comparative analyses of climate change responses (e.g., distribution and phenological changes) among regions with climates that differ in the magnitude of temporal and spatial climatic variation. Data on responses to recent climate change are now available in many regions to facilitate these tests. We provide four recommendations on how to test the predictions reviewed here.

(i) Few studies evaluate how climatic variation at local scales affects the sensitivity and response capacity of populations. If populations are adapted to local climatic variation, then maps of spatial and temporal variation combined with knowledge of how populations are adapted to such variation could make fine-scaled predictions about the vulnerability of populations to climate change possible, rather than being limited to broader generalizations such as tropical versus temperate regions. We suggest comparing traits (e.g., thermal tolerance breadth) and climate change responses among populations that occur in a similar region but experience different amounts of climatic variation (e.g., forest floor versus canopy [38]). Such studies would help to determine the spatial scale at which the seven predictions presented here are valid and how this varies depending on the life history of the organisms being considered (Box 1).

(ii) We need to understand how spatial and temporal climatic variation interacts to affect climate change vulnerability (see Outstanding Questions). A mosaic of climates with different combinations of spatial and temporal variation occurs across the globe (Figure 1C). In many cases, spatial and temporal variation have opposing effects on the vulnerability of a population, and we do not understand which will dominate. Studies that compare the responses of populations to climate change among areas with similar temporal variation but different spatial variation (or vice versa) will be necessary to understand how spatial and temporal variation interact to affect climate change responses.

(iii) We advocate for more realistic predictive models that incorporate climate data at relevant resolutions and aspects of biology that are sensitive to climatic variation (Box 1, see Outstanding Questions) [88]. Although suitable climate data might not yet be available for all circumstances [7,89], biologists are increasingly gaining access to climate data with finer spatial and temporal resolutions (e.g., [64]). These models will facilitate more accurate predictions of climate change impacts that better inform policy decisions.

(iv) The population-level predictions reviewed here should be expanded to understand vulnerability in communities of interacting species. Such an approach requires understanding both the filtering of species by traits and the evolution of their populations to climates and other species. The evolving metacommunity framework provides one such approach to understanding this complexity [90].

Where Might Populations Be Most Vulnerable

Given the seven predictions presented here, populations living in places with high spatial climatic variation (e.g., mountainous regions, Figure 1) should be less vulnerable to climate change owing to a higher response capacity (Figure 2). These populations often maintain higher genetic variation, and although they might disperse less, they should also track suitable climates more easily. Small populations currently restricted to isolated mountaintops are likely to be an exception. By contrast, species living in climates with less spatial variation (e.g., inland plains) could have lower standing genetic variation, and their higher dispersal propensity might act only to compensate for the greater distances they must travel to find future suitable climates.

The effects of temporal climatic variation are less clear because temporal variation affects sensitivity and response capacity in conflicting ways. Populations experiencing more temporal variation could be less sensitive to climate change and maintain more genetic variation in traits related to climate change resilience, but encounter interruptions to climate-tracking and evolution that increase extirpation risk and reduce genetic variation. Conversely, populations experiencing less temporal climatic variation could be more sensitive to climate change and have less genetic variation, but ecological and evolutionary responses might be more consistent and effective. Resolving these conflicting effects on sensitivity and response capacity will require targeted experiments and models.

Concluding Remarks

Few studies incorporate spatial or temporal variation into experimental designs or predictive modeling. We stress that past, present, and future climatic variation are important ecological and evolutionary forces that shape the sensitivity and response capacity of populations under climate change. Indeed, the predictions we present here are only a subset of the ways in which climatic variation affects vulnerability. Appreciating the significance of climatic variation will significantly improve our understanding and predictions of where and why populations will be vulnerable to climate change.

Outstanding Questions

What is the most relevant spatial and temporal resolution of climate data to predict the response of a population to climate change? Which traits determine the most relevant resolution? Debate exists on the resolution of climate data that will be necessary to accurately predict climate change vulnerability [7,8,89]. Few studies have attempted to determine the most relevant resolution and how that might differ among species (but see [91]). Recent responses of populations to climate change could be used to help determine what climate data resolution best explains observed climate change responses.

How does climatic variation at different resolutions interact to affect climate change vulnerability? Climatic variation at different resolutions can have opposing effects on the vulnerability of populations to climate change (Box 1). However, we know little about how these resolutions interact to affect climate change vulnerability. Experiments and models that expose populations to climatic variation at multiple resolutions will be necessary to address this issue.

How do spatial and temporal climatic variation interact to affect climate change vulnerability? Spatial and temporal variation can have opposing effects on the vulnerability of populations to climate change. Global climates are composed of many combinations of spatial and temporal variation (Figure 1C). It is therefore crucial to resolve how different combinations of spatial and temporal variation will interact to affect climate change vulnerability.

How will changes in spatial and temporal climatic variation affect climate change vulnerability? Climatic variation is likely to change in the future [92]. The literature reviewed here demonstrates that climatic variation affects many aspects of biology. Thus, changes in climatic variation and its predictability will likely affect climate change vulnerability. Future studies will need to accurately account for potential changes in climatic variation to better predict climate change responses.

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Chapter 3: Can Temperature Variation Predict Climate Change Vulnerability at Microgeographic Scales?

ABSTRACT

Climate change could cause the extinction of up to a million species. Predicting where and which species will be most vulnerable to climate change could help direct conservation resources to minimize biodiversity loss. Recently, many studies have suggested that the degree to which temperature varies over time (e.g., daily, seasonal) in a location could help predict the vulnerability of species in different parts of the world. However, we still do not know the spatial scales at which the relationship between climatic variation and vulnerability apply. Here, we test whether differences in climatic variation predict climate change vulnerability at microgeographic scales. Specifically, we use *Daphnia magna* in natural freshwater rock pools with different degrees of temperature variation to test whether: (1) populations from locations with higher temperature variation will have higher critical thermal maximum (CT_{max}); (2) populations from locations with (a) higher within-generation temperature variation and (b) higher within-generation temperature predictability will have higher CT_{max} plasticity; and, (3) populations from locations with higher between-generation temperature variation will have higher genetic variation in CT_{max}. Although we observed genetic differences in CT_{max} plasticity and genetic variation in CT_{max} among *D. magna* clones, neither plasticity or genetic variation were explained by differences in climatic variation among pools as predicted by local adaptation to temperature variation. High gene flow enhanced by hybrid vigor and weak selection likely explain why we did not observe microgeographic adaptation to differences in temperature variation. Moreover, our results suggest that the genetic variation and plasticity in CT_{max} we observed in *D. magna* is unlikely sufficient to reduce the impacts of climate change. CT_{max}

plasticity was minimal and genetic variation in CT_{max} was 87% lower when *D. magna* developed at high temperatures. More studies are needed to determine the scales at which differences in temperature variation are likely to affect the vulnerability of species to climate change and what ecological factors affect those scales.

INTRODUCTION

Species around the globe are shifting their distributions, reducing their body size, and changing the timing of important life events to cope with changing climates (Chen et al. 2011, Gardner et al. 2011, Socolar et al. 2017). As climate change accelerates, these responses are unlikely to keep pace for many species, which could make them vulnerable to extinction. Indeed, 16% of species could go extinct if greenhouse gas emissions continue unabated (Maclean and Wilson 2011, Urban 2015). Such large-scale extinction could substantially affect ecosystems and human wellbeing (Cardinale et al. 2012, Hooper et al. 2012). Predicting where and which species will be most vulnerable to climate change could help direct conservation resources to minimize biodiversity loss.

Predicting climate change vulnerability requires an understanding of three important factors (Dawson et al. 2011, Beever et al. 2016, Nadeau et al. 2017): (1) the degree of local climate change (i.e., exposure), (2) the degree to which climate change will reduce the fitness of focal species (i.e., sensitivity), and (3) the ability of species to mitigate fitness reductions through range shifts, plasticity, and evolutionary adaptation (i.e., response capacity). Our understanding of exposure is rapidly improving as biologists and climate scientists make more detailed predictions of important climate variables at fine spatial and temporal resolutions (Lenoir et al. 2017, Zellweger et al. 2019). Understanding and predicting sensitivity and response capacity is more difficult without detailed studies of specific biological and landscape contexts (Dawson et

al. 2011, Urban et al. 2016). However, recent research is suggesting that the degree to which temperature varies over time (e.g., daily, seasonal variation) in a location could help predict sensitivity and response capacity of species in different parts of the world (Nadeau et al. 2017).

We have long known that species are often adapted to the amount of climatic variation they experience (Scholander et al. 1950, Cohen 1966, Janzen 1967, Levins 1968). For example, in 1967 Janzen suggested that tropical species evolved narrower temperature tolerances than temperate species because tropical species experience low seasonal temperature variation. He then suggested that narrower temperature tolerances make tropical species more sensitive to cool temperatures in mountain passes. In other words, Janzen suggested we could predict a species' sensitivity to temperature change based on the degree of seasonal temperature variation they experience. Multiple studies have now confirmed this result (Ghalambor et al. 2006, Sunday et al. 2010, Khaliq et al. 2014) and used the same logic to demonstrate that tropical species are more sensitive to temperature increases under climate change relative to temperate species. This research has led to the somewhat counterintuitive prediction that tropical species will be more vulnerable to climate change, despite much greater increases in temperature in temperate regions (Deutsch et al. 2008, Vasseur et al. 2014).

Although this is the best-known example, climatic variation affects many other aspects of a species sensitivity and response capacity under climate change (Nadeau et al. 2017). For example, species often evolve plasticity to cope with predictable temperature variation (Schlichting and Pigliucci 1998, Botero et al. 2015, Tufto 2015). Such plasticity is likely responsible for many of the phenological and body-size changes already observed in response to climate change (Merilä and Hendry 2014). When climatic variation occurs among generations, species often have higher genetic variation (Botero et al. 2015, Huang et al. 2015, Diamond

2017), which can increase evolutionary potential and therefore decrease climate change vulnerability (Kelly et al. 2003, Mariac et al. 2016). These relationships between climatic variation and climate change vulnerability could also help predict where climate change will have the greatest impacts.

However, before we can use the degree of climatic variation in a region to predict climate change vulnerability, it is important to understand the scales at which these relationships apply. Most studies testing for relationships between climatic variation and vulnerability use among-species comparisons at broad-spatial scales (Deutsch et al. 2008, Hof et al. 2012, Krenek et al. 2012, Vasseur et al. 2014, Simon et al. 2015, Diamond 2017). However, climatic variation often differs at fine-spatial scales. For example, temperature variation differs dramatically between aboveground and belowground habitats and between shallow and deep belowground habitats (Mammola et al. 2019). Springs in lakes or rivers can create areas with little temperature variation relative to the surrounding water (Johansson and Laurila 2017). Also, temperature variation increases substantially from the soil to the canopy of tropical wet forests (Scheffers et al. 2017). Adaptation to such fine-scale climatic variation might occur despite gene flow, a phenomenon known as microgeographic adaptation (Richardson et al. 2014). If species exhibit microgeographic adaptation to climatic variation, we could make fine-scaled predictions of climate change vulnerability that would improve the design of conservation strategies.

We might expect adaptation to climatic variation at fine-spatial scales for two reasons. First, we know that sensitivities and response capacities can differ among populations within a species at regional scales depending on the climatic variation they experience (Krenek et al. 2012, Yampolsky et al. 2014, Heerwaarden et al. 2016a, Brahim et al. 2019, Healy et al. 2019). For example, critical thermal maxima (i.e., a common measure of sensitivity to temperature

change; CT_{max}) and CT_{max} plasticity (i.e., a measure of response capacity) differ among tropical and temperate populations of *Drosophila melanogaster* as predicted based on regional differences in climatic variation (Heerwaarden et al. 2016a). Second, other species demonstrate microgeographic adaptation to temperature, despite gene flow (Skelly and Freidenburg 2000, Freidenburg and Skelly 2004, Skelly 2004, Richter-Boix et al. 2015, Johansson et al. 2016). For instance, life history traits and CT_{max} of wood frogs (*Rana sylvatica*) often differ among ponds just a few hundred meters apart, which experience different amounts of temperature variation due to differences in forest canopy cover (Skelly and Freidenburg 2000, Freidenburg and Skelly 2004, Skelly 2004). Moreover, differences among ponds can evolve rapidly (Skelly and Freidenburg 2000). Hence, microgeographic adaptation to climatic variation at very fine-spatial scales might be more common than generally appreciated.

Here, we test for microgeographic adaptation to climatic variation in *Daphnia magna* (a small crustacean) from freshwater rock pools within a 1.9 ha study area. Temperature variation differs substantially among pools separated by 1 – 250 m (Fig. 1). We use lab-based common-garden experiments to test the following predictions (Fig. 2): (P1) populations from locations with higher temperature variation, and therefore higher maximum temperatures, will have higher CT_{max}; (P2) populations from locations with (a) higher within-generation temperature variation and (b) higher within-generation temperature predictability will have higher CT_{max} plasticity; and, (P3) populations from locations with higher among-generation temperature variation will have higher genetic variation in CT_{max}. We then use a field-based artificial warming experiment to evaluate whether potential differences in CT_{max}, CT_{max} plasticity, and genetic variation in CT_{max} result in differences in vulnerability to warming.

METHODS

Study System:

We focus on a metapopulation of *Daphnia magna* that occurs in freshwater rock pools in Acadia National Park, Maine, USA. Freshwater rock pools are depressions in bedrock that fill with rainwater and are an ideal system to test the above predictions for several reasons. First, the degree of daily and seasonal temperature variation differs significantly among pools that are only meters apart due to differences in depth and solar exposure (Fig. 1). Second, water in freshwater rock pools is shallow (mean depth = 24 cm) and well mixed by coastal winds. Therefore, water temperature is often homogeneous throughout a pool, which makes local adaptation more likely because species are unable to avoid extreme temperatures with behavioral thermoregulation (Gunderson and Stillman 2015). Last, we can replicate the entire freshwater rock pool ecosystem in field mesocosms and simulate climate change in those mesocosms using open-top greenhouses (see below).

Daphnia magna is important in freshwater ecosystems due to its role as a primary consumer of algae and because it is prey for many secondary consumers. *Daphnia magna* is also an ideal focal species because we know *D. magna* evolves rapidly in response to temperature changes (De Meester et al. 2011, Geerts et al. 2015, Brans et al. 2017). Moreover, *D. magna* CTmax is often adapted to maximum temperatures experienced at regional scales (Yampolsky et al. 2014, Fields et al. 2015, Seefeldt and Ebert 2019) and *D. magna* populations are often genetically structured at microgeographic scales (De Meester 1996, Haag et al. 2005, 2006). Hence, *D. magna* is a good candidate to observe microgeographic adaptation in CTmax. In addition, *Daphnia* undergo clonal reproduction throughout most of their lives, which allows us to

maintain genetically constant lines in the lab and use a split-brood design to measure plasticity and genetic variation in CT_{max}.

Temperature Variation in Focal Pools:

We focused on 10 pools that differed in temperature variation (Fig. 1). We measured daily maximum temperature in each pool between 15 June and 15 October 2018 (the primary growing season for *D. magna* in our study site) using temperature data loggers (models: HOBO Pendant UA-001-08 or Onset Hobo U20L) placed in the deepest part of the pool and covered with a rock to block direct sunlight. We used these data to calculate the average maximum temperature in the hottest month (August), the daily standard deviation in maximum temperature across the season (i.e., within-generation variation), the predictability of daily maximum temperature (i.e., within-generation predictability), and the total temperature range (i.e., among-generation variation; Fig. 1). We focus on maximum temperature because we expect *D. magna* CT_{max} to be associated with maximum temperature (Yampolsky et al. 2014). We used generalized least squares to estimate the daily standard deviation and predictability of maximum temperature for each pool. This method allowed us to remove the seasonal component of the temperature variation when calculating the daily standard deviation, while also estimating the daily predictability by fitting a Gaussian variogram model to the residuals. The variogram model estimates the number of days over which temperature measurements are autocorrelated (i.e., the variogram range), which is a measure of predictability. We fit the generalized least squares independently to each temperature time series using the ‘*gls*’ function in the ‘*nlme*’ package (Pinheiro et al. 2015) in R version 3.6.0. We fit a quadratic model with daily maximum temperature as the response variable, Julian date as a quadratic covariate, and specified the temporal correlation structure using a Gaussian variogram model. The quadratic model removes

the seasonal component of the temperature variation before estimating the daily standard deviation and predictability. We estimated the daily standard deviation as the standard deviation of the residuals from the model and the predictability as the range of the variogram model. The focal pools differed substantially in all measures of temperature variation (Fig. 1).

Daphnia Collection and CTmax Assays:

We collected *D. magna* from 10 pools in total using either a dip net or a plastic pipette. In 2017, we collected one to eight adult females from each of six pools, and in 2018 we collected 25 adult females from each of eight pools, including four pools sampled in 2017. We consider each female collected to be a separate clone. This assumption may not be strictly true due to clonal reproduction. However, we collected females shortly after ephippia hatched in the spring, which is when clonal variation is highest. We kept each female in the lab in separate 100 ml specimen cups filled with 80 ml of water from a local freshwater rock pool that we filtered through 500- μ m mesh to remove invertebrates. We kept each cup at room temperature under natural light and added water containing algae daily. Once the females produced a brood, we haphazardly selected two neonates to continue the clonal line and measure CTmax in the lab and four neonates from each of 20 females per pool to include in our artificial warming experiment (2018 only, see below).

We let the two neonates from each clone grow in separate 120 ml specimen cups filled with 100 ml of filtered and sterilized water from a local stream. We kept each cup in a 20°C incubator with a 16:8 light:dark cycle. Every two to three days we fed each individual 200 μ l of algae culture with a standardized density of 37.5×10^6 cells/ml and checked to see if they had produced a brood. When they produced a brood, we haphazardly separated two neonates to continue the clonal line. We repeated this process for at least two generations to reduce maternal

effects. In the final cycle, we split the brood from each clonal line and put two to three neonates in a 20°C incubator and two to three neonates in a 25°C incubator in separate 120 ml specimen cups. We grew all clones at both temperatures to measure the degree to which CTmax changed based on the developmental temperature (i.e., CTmax plasticity). We chose 20°C because average daily mean temperature between June and October in the 10 focal pools was 20.0°C (SD = 3.5°C). We chose 25° to represent 5°C of potential warming, which is the predicted change in air temperature under a high emissions scenario in our study area by the end of the century (Lynch et al. 2015). We grew all individuals at these temperatures until they were 14 – 30 days old, feeding them as described above and removing any neonates produced every two to three days.

We measured CTmax on the mature females by putting each female in a 5 ml glass beaker containing 5 ml of water and suspended the beakers in a water bath with an initial temperature of approximately 22.5°C. We raised the temperature 0.5°C per minute and recorded the temperature when each individual lost equilibrium and sank to the bottom. We measured the CTmax of an average of 15.2 (SD = 5.5) individuals per trial including a random assortment of individuals from each developmental temperature. In total, we measured CTmax on 563 individuals that originated from 131 clones, with an average of 13.1 (SD = 5.6; Supplemental Table S1) clones per pool. The number of clones per pool is less than the number of females we collected because some clones died or produced males in the lab, which ended their clonal line. Clonal loss in the lab could affect our results, especially if we observed high clonal loss in pools with extremely warm or cool temperatures. However, we observed the highest clonal loss in moderate-temperature pools (Supplemental Table S1) and removing the pools with the highest clonal loss from our analysis did not affect our conclusions (Supplemental Material).

Artificial Pools:

We used artificial rock pools to estimate climate change vulnerability for the eight *D. magna* populations sampled in 2018. In early June 2018, we installed 16 artificial rock pools (eight controls and eight warmed) in two groups within our study area. We used 64 L (68 cm long, 46 cm wide, 32 cm deep) plastic tubs insulated with R-10 rigid foam insulation and surrounded each pool with large rocks. We filled the pools with 12 L of water from each of three natural pools (36 L total) that we filtered through 500- μ m mesh to remove invertebrates, including all life stages of *D. magna*. We fitted half the pools (warmed treatment) with an open-top greenhouse that we constructed with 1-mm Sun-Lite® HP solar glazing (Solar Components Corporation). We fitted the remaining pools (controls) with a top similar in shape to the greenhouses, but made of screen to control for possible effects of the top. We put a temperature data logger in each pool. We seeded each warmed-control pair of artificial pools with *D. magna* neonates from one of the eight natural pools sampled in 2018 (see Fig. 1 for the temperatures in these pools). Both the warmed and the control pools in a pair received two *D. magna* neonates from each of 20 females collected from the natural pool in 2018 (40 neonates total for each pool). Neonates from each female are clones and therefore each control-warmed pair started with a genetically identical set of 40 *D. magna* neonates. We also added two ostracods from each of three natural pools (six total) to increase the reality of the invertebrate community. Many other rock pool organisms colonized the pools naturally, including: *Ceriodaphnia dubia*, *Chydorus sphaericus*, Calanoid copepods (Order: *Calanoida*), Cyclopoid copepods (Order: *Cyclopoida*), non-biting midges (Family: *Chironomidae*), water boatman (*Trichocorixa verticalis*), mosquitos (*Aedes sp.*), aquatic springtails (*Podura aquatica*), and water mites (Order: *Trombidiformes*). In September 2018 (95 days after initiation), we sampled invertebrates using a dip-net with 500- μ m

mesh following a standardized sweep pattern in each pool to ensure equal sampling effort. The sweep pattern included moving the net around the pool perimeter and then three times across the length of the pool. We preserved the samples in 70% ethanol and counted the number of adult female *D. magna* in each sample under a microscope in the lab. We predicted that the *D. magna* from natural pools with more temperature variation would have higher abundance in the warmed relative to the control pools, given that high temperature variation can result in lower sensitivity and higher response capacity.

Statistical Analysis:

We compared a suite of Bayesian linear mixed-effects models to evaluate the predictions described above using approximate leave-one-out cross validation in the ‘*loo*’ package in R (Vehtari et al. 2017) and Bayesian stacking weights (Yao et al. 2018). Bayesian stacking estimates weights for each model that minimize the leave-one-out prediction error of weighted-average predictions from all models in the model set. Models with weights close to zero provide poor out-of-sample prediction, while models with weights close to one (100%) provide the best out-of-sample prediction relative to other models in the model set. Bayesian stacking weights provide a useful tool for model selection when models have similar predictive ability, and therefore similar expected log predicted densities (ELPD), or when there is high uncertainty in the ELPD differences among models.

First, we separately analyzed the CTmax data from individuals that developed at 20°C and 25°C to evaluate if there is genetic variation in CTmax, whether genetic variation in CTmax is due to microgeographic adaptation to local temperature variation, and whether the conclusions differed depending on developmental temperature in the lab (Table 1). We first fit a null model with CTmax as the response variable, year of the experiment as a fixed effect, and a random

effect for CTmax trial, but no effect of clone or pool (M1-0). This null model represents the case where there are no differences in CTmax among clones (i.e., there is no genetic variation in CTmax). We included year in the model to account for potential differences in CTmax among years, which could occur if there were unquantified differences in water, algae, or light quality among years in the lab. We fit year as a fixed effect because there were too few levels ($n = 2$) to estimate the random-effect variance. We next added a clone random effect to the null model, which represents the case where there is genetic variation in CTmax, but no microgeographic adaptation (M1-1). We then used two different models to evaluate whether there was microgeographic adaptation in CTmax as predicted (P1; Fig. 2). First, we added a pool fixed effect to M1-1, to evaluate whether the average CTmax differed among pools (M1-2). Here we fit pool as a fixed effect because we were interested in the differences among our focal pools specifically. Second, we added the average maximum pool temperature in the warmest month as a fixed effect and pool as a random effect to M1-1 to evaluate if CTmax increased with maximum pool temperature as predicted (M1-3). Last, we modified M1-1 such that the variance of the clone random effect differed among pools (M1-4), which represents the case where genetic variation differs among pools (P3; Fig. 2). We fit each of the genetic variances separately as fixed effects.

Second, we analyzed the CTmax data from individuals that developed at 20°C and 25°C together to test for plasticity in CTmax, genetic variation in plasticity, and whether genetic variation in plasticity is due to microgeographic adaptation (P2a and b; Fig. 2). We first fit a null model with a year fixed effect and clone and trial random effects to represent the case where there is no plasticity in CTmax (M2-0). We then added a fixed effect for developmental temperature in the lab (20°C or 25°C) to the null model to test for plasticity in CTmax (M2-1).

We next allowed the developmental temperature effect to vary randomly among clones (i.e., a random slope model) to represent the case where plasticity differed among clones (i.e., genetic variation in plasticity; M2-2). We used three different models to evaluate whether there is microgeographic adaptation in CTmax plasticity. First, we added a pool fixed effect and an interaction between pool and developmental temperature to M2-2 to evaluate if the average plasticity among clones differed among pools (M2-3). Second, we added a daily temperature variation fixed effect, an interaction between daily temperature variation and developmental temperature, and a pool random effect to M2-2 to evaluate if plasticity increased with daily temperature variation as predicted (M2-4; P2a; Fig. 2). Last, we added a daily temperature predictability fixed effect, an interaction between daily temperature predictability and developmental temperature, and a pool random effect to M2-2 to evaluate if plasticity increased with daily temperature predictability as predicted (M2-5; P2b; Fig. 2).

We analyzed the abundance of *D. magna* in the artificial rock pools by first subtracting the number of *D. magna* in the control from the number in the warmed pool for each of the eight pairs. Using this difference as the response variable allowed us to model the response as normally distributed and therefore alleviate issues with overdispersion of count data. It also controlled for any potential differences in how *D. magna* from different natural pools responded to the artificial-pool setting. We fit four separate models with the difference in abundance as the response variable and one of the following fixed effects: (1) maximum temperature, (2) daily temperature variation, (3) daily temperature predictability, and (4) seasonal temperature range. We considered the fixed effects significant if the 95% credible interval of the coefficient did not overlap zero.

We fit all models in JAGs using the ‘*R2jags*’ package in R version 3.6.0. In the models where genetic variation differed among pools, we used three chains, each with 30,000 MCMC iterations, a burn-in period of 25,000 iterations, and retained every fifth draw. For all other models, we used three chains with 10,000 iterations, a burn-in period of 5000 iterations, and retained every fifth draw. These MCMC settings resulted in well-mixed chains as assessed visually and by evaluating whether the Gelman-Rubin statistic was < 1.1 . We used vague normal priors with a mean equal to zero and precision equal to 0.001 for all coefficients. We used vague gamma priors with rate and shape parameters set to 0.001 for all variance terms. Posterior predictive checks on the top models from the two sets of analyses confirmed that the models fit the data well (Hobbs and Hooten 2015). In all cases, Bayesian p-values (i.e., goodness of fit statistics) for the mean and variance of the data were between 0.495 and 0.533, suggesting the models fit the data well.

RESULTS

Microgeographic Adaptation:

When *D. magna* developed at 20°C, CTmax ranged between 35.0°C and 39.1°C among the 296 individuals tested (mean = 37.5°C, SD = 0.6°C). CTmax was 0.9°C (95% credible interval [CI] = 0.6 – 1.1°C) higher in 2018 relative to 2017. The top model (M1-1) received 52.6% of the stacking weight and included genetic variation in CTmax, but no microgeographic adaptation or differences in genetic variation among pools (Table 1; Fig. 3). The percent of phenotypic variation explained by differences among clones (i.e., heritability) from this model was 19.9% (95% CI = 3.3 – 36.1%). The model including differences in genetic variation among pools (M1-4) received 42.9% of the stacking weight (Table 1), suggesting possible differences in genetic variation among pools. However, genetic variation was similar in most pools and did not

increase with the seasonal temperature range in the pool of origin as predicted (Fig. 4). The remaining models each received $\leq 5.5\%$ of the stacking weight. Hence, we concluded that although there is genetic variation in CTmax in the metapopulation, genetic variation is not maintained by differences in temperature variation among pools as predicted.

When we raised *D. magna* at 25°C, CTmax ranged between 36.2°C and 39.5°C among the 266 individuals tested (mean = 38.1°C, SD = 0.5°C). CTmax was 0.5°C (95% CI = 0.3 – 0.8°C) higher in 2018 relative to 2017. The top model (M1-3) received 51.1% of the stacking weight and included the effects of pool temperature on CTmax (Table 1; Fig. 3). However, the relationship between CTmax and pool temperature was opposite that predicted based on the temperature variation in the pool of origin (Figs. 2 and 3) and the 95% credible interval of the slope overlapped zero (mean slope = -0.035, 95% CI = -0.091 - 0.020). The next best model received 48.9% of the stacking weight (Table 1) and suggested there was no genetic variation among clones (M1-0). Further supporting this model, estimates of genetic variation and heritability from model M1-1 were low when individuals developed at 25°C. The median variation among clones was 0.042 (95% CI = 0.007 – 0.086) when individuals developed at 20°C, but only 0.005 (95% CI = 0.001 – 0.030) when individuals developed at 25°C. CTmax heritability was only 2.6% (95% CI = 0.3 – 14.7%) when individuals developed at 25°C, which is an 87% reduction in heritability relative to that estimated at 20°C. The remaining models did not receive any stacking weight. Hence, we conclude that there was no microgeographic adaptation in CTmax and little or no genetic variation in CTmax when individuals developed at 25°C.

The top model from the suite of models used to evaluate plasticity (M2-1) received 48.3% of the stacking weight and included plasticity, but no genetic variation in plasticity (Table

2). On average, CT_{max} was 0.4°C (95% CI = 0.3 – 0.5°C) higher when *D. magna* developed at 25°C relative to 20°C (Fig. 3). The model suggesting plasticity differed depending on the pool temperature (M2-3) received 42.4% of the stacking weight. However, the 95% credible interval of the interaction term describing the relationship between plasticity and the predictability of pool temperature overlapped zero (95% CI = -0.240 – 0.894), which suggests no strong relationship. The remaining models each received $\leq 9.3\%$ of the stacking weight. Hence, we conclude there is plasticity in CT_{max}, but no microgeographic adaptation in CT_{max} plasticity as predicted.

Artificial Pools:

Between June and September 2018, maximum and minimum water temperatures in the warming treatments were 2.5°C (SE = 0.01°C) and 0.6°C (SE = 0.002°C) warmer than controls, respectively. Maximum temperatures reached a high of 32.7°C in warmed pools versus 30.1°C in control pools. The difference in *D. magna* abundance between warmed and control pools was not associated with the temperature of the natural pool where the *D. magna* originated (Fig. 5). The 95% credible interval of the coefficient for all four temperature variables overlapped zero: (1) 95% CI of maximum temperature coefficient = -55.5 – 49.9, (2) 95% CI of the daily temperature variation coefficient = -58.3 – 48.1, (3) 95% CI of the daily temperature predictability coefficient = -43.6 – 62.6, and (4) 95% CI of the seasonal temperature range coefficient = -54.9 – 48.9. Moreover, we found no difference in *D. magna* abundance between warmed and control pools (paired t-test: $t = -0.832$, $df = 7$, $p = 0.930$), suggesting *D. magna* were not sensitive to the ~2.5°C increase in maximum temperature in the warming treatment.

DISCUSSION

Here we used *D. magna* in freshwater rock pools to evaluate whether a species' sensitivity and response capacity to temperature change are adapted to temperature variation at microgeographic scales. Temperature variation differed substantially among the ten freshwater rock pools we sampled due to differences in solar exposure and water depth. For example, pools less than 1 m apart differed in absolute maximum temperature in 2018 by 7.1°C, which is similar to the temperature difference expected over a 1200 m change in elevation or a 131 km change in latitude in the region. Although we observed differences in CT_{max} and CT_{max} plasticity among *D. magna* clones, our results suggest this genetic variation was not due to microgeographic adaptation as predicted (Figs. 2 and 3). Results from our artificial warming experiment confirmed lab-based results by showing no difference in the vulnerability to warming for *D. magna* populations that originated from different natural pools (Fig. 4). These results also suggest that *D. magna* were insensitive to the 2.5°C of warming in our warming treatment.

Despite no microgeographic adaptation, we did observe developmental plasticity and genetic variation, which suggests some ability for *D. magna* to respond to increased temperatures under climate change. However, our results also suggest those responses might be limited. We observed a 0.4°C increase in CT_{max} with a 5°C increase in mean developmental temperature. This plastic response is similar to that observed in a global review of CT_{max} plasticity, but low for crustaceans included in that review (Gunderson and Stillman 2015). Such small effects are unlikely to reduce the vulnerability of most species to climate change (Gunderson and Stillman 2015, Gunderson et al. 2017). Plasticity might be higher in nature where fluctuating temperatures can result in hardening effects, however, studies in *Drosophila* suggest these effects are small and unlikely to decrease climate change vulnerability (Heerwaarden et al. 2016a).

We also observed genetic variation that could facilitate CT_{max} evolution under climate change. When *D. magna* developed at 20°C, heritability of CT_{max} was similar to the average (0.28, 95% CI = 0.19 – 0.39) from a global review of heritability in upper thermal tolerances (Diamond 2017). However, when *D. magna* developed at 25°C, heritability decreased 87% and the top model suggested no genetic variation in plasticity. Consequently, evolutionary potential might decrease as temperatures warm. The decrease in evolutionary potential was due to a decrease in phenotypic variation among clones, which suggests development at high temperature or the heat-stress response causes genotypes to converge on a similar phenotype. More research is needed to understand the mechanism causing this phenotypic convergence. Changes in heritability among environments, including among different temperatures, are common. However, there are no predictable patterns in the direction of heritability changes given environmental changes (Hoffmann and Merilä 1999). For example, studies have observed both increases (Sisodia and Singh 2009, Heerwaarden et al. 2016b) and decreases (Bennington and McGraw 1996, Ketola et al. 2012, Chirgwin et al. 2015) in genetic variation or heritability under increased temperatures. More research is needed to understand the effects of climate change on heritability to facilitate predictions of when and where we might expect evolution to alter species' responses. Moreover, these results highlight the need to estimate heritability in projected future environments to accurately estimate evolutionary potential (Chirgwin et al. 2015, Heerwaarden et al. 2016a).

The lack of microgeographic adaptation in *D. magna* in our study system is somewhat surprising given what we know about the evolutionary potential of *D. magna* and population genetic structure in other parts of *D. magna*'s range. *Daphnia magna* can evolve rapidly in response to differences in temperature. Experiments with *D. magna* in lab and field mesocosms

that increased temperatures by 4°C demonstrated rapid evolution of population growth rate and size at maturity in as little as three months (Van Doorslaer et al. 2009a, 2010, De Meester et al. 2011). *Daphnia magna* is also one of the only species with documented CT_{max} evolution in response to recent climate change in nature (Geerts et al. 2015) and CT_{max} has also evolved in response to urban heat island effects (Brans et al. 2017). Moreover, *D. magna* CT_{max} is locally adapted to maximum temperatures across its range in Afro-Eurasia (Yampolsky et al. 2014, Seefeldt and Ebert 2019). Genetic studies also commonly reveal population differentiation at fine-spatial scales (Vanoverbeke and De Meester 1997, Haag et al. 2005, 2006, Orsini et al. 2012, 2013). For example, *D. magna* populations that occur in a very similar freshwater rock pool ecosystem as that studied here, show high levels of genetic differentiation even among pools just a few meters apart (Haag et al. 2005, 2006). This population differentiation is often associated with low gene flow and differences in local environments (Haag et al. 2006, Orsini et al. 2013). Last, even if dispersal among populations is high, gene flow that could erode microgeographic adaptation might be limited by the predominance of locally-adapted genotypes that monopolize resources and limit effective immigration of foreign genotypes (Boileau et al. 1992, De Meester et al. 2002, 2016). Indeed, multiple studies with *D. magna* have demonstrated this phenomenon known as population monopolization (De Meester et al. 2002, Van Doorslaer et al. 2009b, Orsini et al. 2013). Together, these aspects of *D. magna* populations suggest microgeographic adaptation to temperature and temperature variation might be likely.

Why then did we not observe microgeographic adaptation in *D. magna* sensitivity and response capacity as predicted? One reason might be the well-known effect of founder events and genetic drift in structuring *Daphnia* metapopulations (Haag et al. 2005, 2006, Orsini et al. 2013). In other freshwater rock pool metapopulations, approximately 16% of *D. magna*

populations go locally extinct annually (Pajunen and Pajunen 2003). Recolonization often occurs by just one to three individuals that rapidly increase in abundance through clonal reproduction, which results in strong founder effects (Ebert et al. 2002, Haag et al. 2005). Although these founder effects can result in population differentiation (Haag et al. 2005, 2006), they do not result in microgeographic adaptation because the founders are randomly selected from the metapopulation and populations go extinct prior to gaining the necessary genetic variation for adaptation (Haag et al. 2006). Such metapopulation dynamics might therefore limit microgeographic adaptation in our study system. However, with genetic variation in CT_{max}, founder events might still result in differences in CT_{max} among pools, even if those differences are not associated with temperature. We did not observe such differences: models including differences in CT_{max} or CT_{max} plasticity among pools had little support in our suite of models (Tables 1 and 2). Moreover, local extirpation rates are likely much lower in our system, which limits the impact of repeated founder effects (Haag et al. 2005). Between 2016 and 2019, we did not observe any extirpation of *D. magna* populations in our study area.

Gene flow reinforced by hybrid vigor could also prevent microgeographic adaptation to temperature variation in our study system. Dispersal, especially among nearby pools (including some focal pools in this study), is likely high due to overflow of water from one pool into adjacent pools during heavy rain events (Vanschoenwinkel et al. 2008). Dispersal among more distant pools might also be high if the gulls (Family: *Laridae*) that we regularly observed bathing in the pools transport *D. magna* adults and ephippia among pools. Indeed, gulls are a significant dispersal agent for many other rock pool invertebrates on nearby Appledore Island, Maine (Simonis and Ellis 2014). Our attempts to measure this longer-distance dispersal using 20 uninhabited artificial rock pools in 2016 failed to document *D. magna* dispersal, despite

documenting dispersal of other *Daphnids*. It is unclear whether this suggests longer-distance *D. magna* dispersal is infrequent, or if our methods were inadequate. However, even if dispersal among more distant pools is infrequent, effective gene flow might be high due to hybrid vigor. Infrequent dispersal can result in high effective gene flow in inbred populations if hybrids of inbred residents and immigrants have a strong fitness advantage (Ingvarsson and Whitlock 2000, Ebert et al. 2002, Haag et al. 2005). In other *D. magna* metapopulations, hybrid vigor was estimated to increase the effective rate of gene flow approximately 35 times above what would be predicted by the number of immigrants alone (Ebert et al. 2002). Genomic analysis of *D. magna* individuals from our study system suggests strong inbreeding (D. Ebert personal communication). Hence, hybrid vigor might significantly enhance gene flow in our study system.

Last, weak and variable selection might also result in a lack of microgeographic adaptation. Water temperatures never exceeded *D. magna* CT_{max} in any of our focal pools, and are often more than 5°C below CT_{max}. Therefore, selection might not be strong for higher CT_{max} in warmer pools. Although, if CT_{max} represents a general measure of warm tolerance, temperature may not need to exceed CT_{max} to impose strong selection. Moreover, temperatures vary in all pools on many different time scales including inter-annually, seasonally, and daily. This variation might slow or prevent adaptation to temperature. Indeed, evolution of other species has been affected by temperature variation. For example, wing melanin (a key thermoregulatory trait) in the alpine butterfly *Colias meadii* has evolved slowly in response to recent climate change due to temporal variation in selection (Kingsolver and Buckley 2015). Also, Bonebrake and Deutsch (2012) showed that in temperate regions like our study area, the effect of seasonal temperature variation swamps the effect of spatial temperature variation on adaptation of species temperature tolerances. Moreover, each of our predictions is based on the

effects of temperature variation at a single temporal scale (e.g., daily, seasonal). Yet, we know little about how temperature variation at different temporal scales interacts to affect selection on temperature tolerances.

A large body of research suggests that adaptation to temperature variation at broad-spatial scales results in geographic differences in the sensitivity and response capacity of species to climate change (Nadeau et al. 2017). This geographic pattern is especially evident when comparing species from tropical and temperate locations. However, the question remains if temperature variation regularly affects the sensitivity and response capacity of species at finer-spatial scales. Here, we did not observe adaptation at microgeographic scales, likely due to high gene flow, and weak and variable selection. However, other studies have observed fine-scaled differences in a variety of traits among populations from environments with different amounts of temperature variation, despite gene flow among populations (Skelly and Freidenburg 2000, Freidenburg and Skelly 2004, Skelly 2004, Richter-Boix et al. 2015, Johansson et al. 2016, Brahim et al. 2019). We suspect microgeographic adaptation to temperature variation will be more common in systems where (1) there are very large differences in temperature variation (e.g., thermal springs versus surrounding lake water; [Johansson et al. 2016]) or (2) where selection is very strong (e.g., selection on growth rate in vernal pools; [Skelly 2004]). More studies are needed to determine the scales at which differences in temperature variation are likely to affect the sensitivity and response capacity of species to climate change and what ecological factors affect those scales. Such studies could significantly improve our predictions of which species will be most vulnerable to climate change, where they will be vulnerable, and help guide conservation strategies to minimize biodiversity loss in a changing climate.

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Table 1. Model comparison to evaluate whether there is genetic variation in the critical thermal maximum (CTmax) of *Daphnia magna*, whether genetic variation stems from microgeographic adaptation, and whether the results differ depending on the developmental temperature (20°C or 25°C). We used approximate leave-one-out cross validation and Bayesian stacking weights for model comparison. P_{eff} is the effective number of parameters, ELPD is the expected log predictive density, ΔELPD is the difference in ELPD from the top model, and $\Delta\text{ELPD SE}$ is the standard error in ΔELPD . In the Model column, parameters expressed as (1|x) are random intercept terms, year is the year of the experiment (2017 or 2018), pool is the natural pool of origin, max_temp is the maximum temperature in the pool of origin, and (1|clone_p) is a random effect where the variance among clones (i.e., the genetic variation) is allowed to vary among pools. All models also included a random intercept for the CTmax trial, which is not shown.

Hypothesis	Model	P_{eff}	ELPD	ΔELPD	$\Delta\text{ELPD SE}$	Stacking Weight
20°C						
M1-1: Genetic var.	CTmax ~ year + (1 clone)	62.5	-196.9	0.0	0.0	0.526
M1-4: Genetic var. differs among pools	CTmax ~ year + (1 clone _p)	64.8	-197.4	-0.5	2.3	0.419
M1-0: No genetic var.	CTmax ~ year	27.3	-204.3	-7.4	3.8	0.055
M1-3: Microgeographic adaptation	CTmax ~ year + max_temp + (1 pool) + (1 clone)	63.6	-198.4	-1.5	0.8	0.000
M1-2: Microgeographic adaptation	CTmax ~ year + pool + (1 clone)	67.5	-201.8	-4.9	2.4	0.000
25°C						
M1-3: Microgeographic adaptation	CTmax ~ year + max_temp + (1 pool) + (1 clone)	32.7	-170.2	0.0	0.0	0.511
M1-0: No genetic var.	CTmax ~ year	22.5	-170.2	-0.1	2.5	0.489
M1-1: Genetic var.	CTmax ~ year + (1 clone)	30.5	-170.8	-0.6	2.3	0.000
M1-4: Genetic var. differs among pools	CTmax ~ year + (1 clone _p)	44.1	-172.5	-2.4	2.1	0.000
M1-2: Microgeographic adaptation	CTmax ~ year + pool + (1 clone)	37.9	-174.0	-3.8	1.8	0.000

Table 2. Model comparison to evaluate whether there is plasticity in the critical thermal maximum (CTmax) of *Daphnia magna*, genetic variation in that plasticity, and microgeographic adaptation. We used approximate leave-one-out cross validation and Bayesian stacking weights for model comparison. P_{eff} is the effective number of parameters, ELPD is the expected log predictive density, ΔELPD is the difference in ELPD from the top model, and $\Delta\text{ELPD SE}$ is the standard error in ΔELPD . In the Model column, year is the year of the experiment (2017 or 2018), dev_temp is the developmental temperature (20°C or 25°C), pool is the natural pool of origin, pool_temp_SD is the daily variation in maximum temperature, and pool_temp_pred is the predictability of daily temperature variation. Parameters expressed as (y|x) are random slope terms where the slope for y varies among levels of x. Parameters expressed as (1|x) are random intercept terms. All models also included a random intercept for the CTmax trial, which is not shown.

Hypothesis	Model	P_{eff}	ELPD	ΔELPD	$\Delta\text{ELPD SE}$	Stacking Weight
M2-1: Plasticity	CTmax ~ year + dev_temp + (1 clone)	65.0	-364.4	0.0	0.0	0.483
M2-5: Microgeographic adaptation	CTmax ~ year + dev_temp * pool_temp_pred + (dev_temp clone) + (1 pool)	72.7	-365.1	-0.7	3.1	0.424
M2-0: No plasticity	CTmax ~ year + (1 clone)	59.1	-396.2	-31.7	8.7	0.093
M2-2: Genetic var. in plasticity	CTmax ~ year + dev_temp + (dev_temp clone)	72.0	-365.4	-0.9	0.8	0.000
M2-4: Microgeographic adaptation	CTmax ~ year + dev_temp * pool_temp_SD + (dev_temp clone) + (1 pool)	73.3	-365.6	-1.2	3.1	0.000
M2-3: Microgeographic adaptation	CTmax ~ year + dev_temp * pool + (dev_temp clone)	75.5	-368.3	-3.9	3.7	0.000

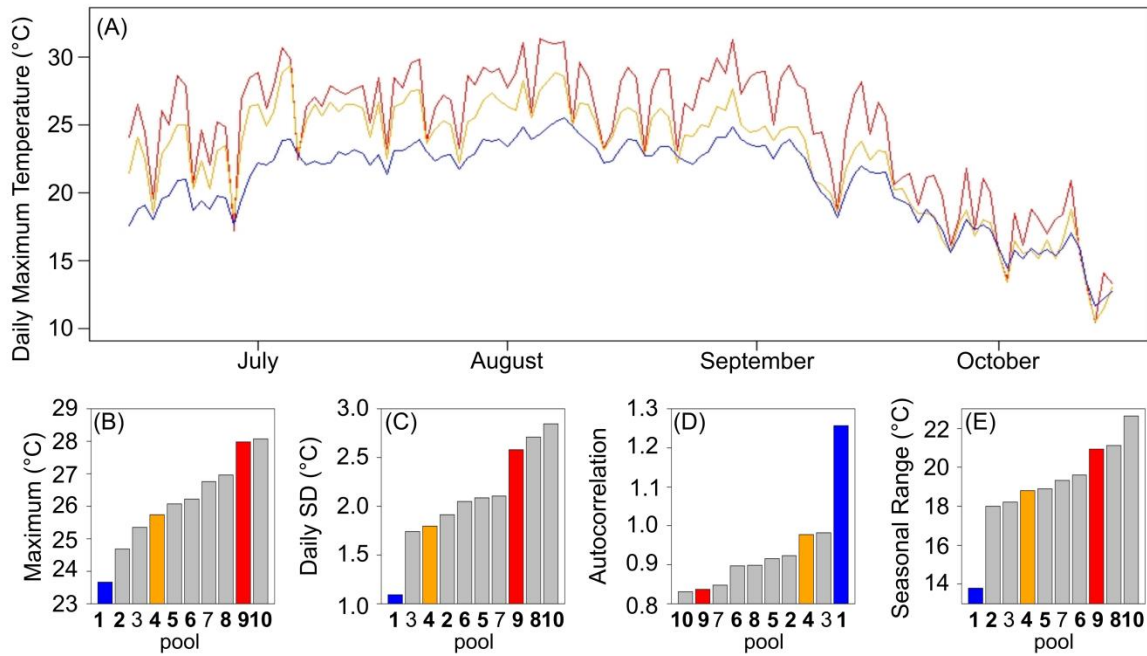


Figure 1. Differences in water temperature variation in 10 focal freshwater rock pools used to test for microgeographic adaptation in *Daphnia magna*. (A) Time series of daily maximum temperature between June 15 and October 15, 2018 from three pools (pool 1, blue; pool 5, orange; pool 10, red) with different amounts of temperature variation. Differences in (B) maximum temperature, (C) daily variation in maximum temperature, (D) the predictability of maximum temperature (higher autocorrelation equals higher predictability), and (E) seasonal temperature range for each of the 10 focal pools. Red, orange, and blue bars in lower plots correspond to the colored lines in (A). Pools numbered in bold in B-E are pools where we sampled *D. magna* in 2018 to use in our artificial warming experiment.

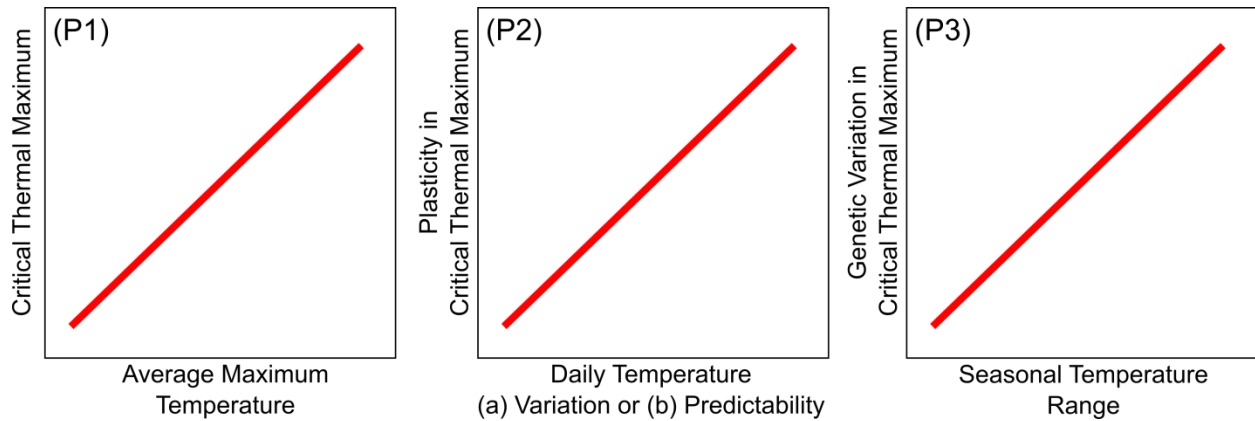


Figure 2. Predicted relationships between the traits of *Daphnia magna* that originate from freshwater rock pools with different amounts of temperature variation. (P1) Populations from locations with higher temperature variation, and therefore higher maximum temperatures, will have a higher critical thermal maximum. (P2) Populations from locations with (a) higher within-generation temperature variation and (b) higher within-generation temperature predictability will have higher critical thermal maximum plasticity. (P3) Populations from locations with higher between-generation temperature variation will have higher genetic variation in critical thermal maximum.

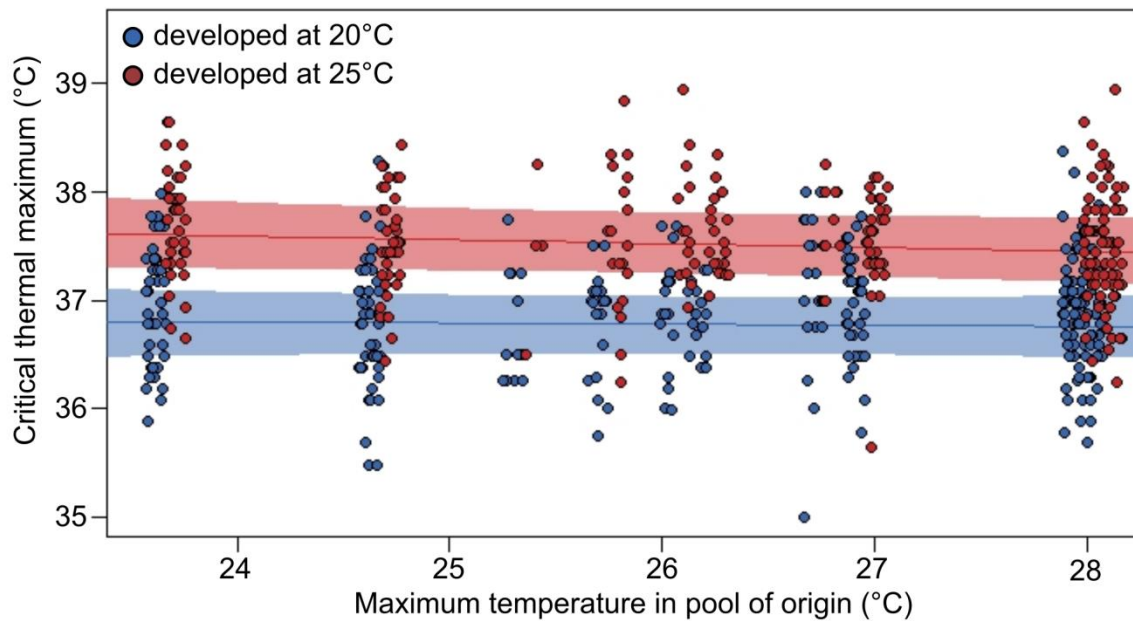


Figure 3. Critical thermal maximum (CTmax) and CTmax plasticity of *Daphnia magna* from 10 freshwater rock pools with different maximum water temperatures. Points are CTmax values from individuals that developed at 20°C (blue) and 25°C (red), and differences between blue and red points show plasticity. We adjusted values for the experiments conducted in 2018 based on a year effect estimated from a Bayesian mixed-effects model (see Results). Points are jittered around the true x-value to better visualize the data. Shaded areas (95% credible intervals) and horizontal lines (median) show the estimated relationship between CTmax and maximum temperature in the pool of origin.

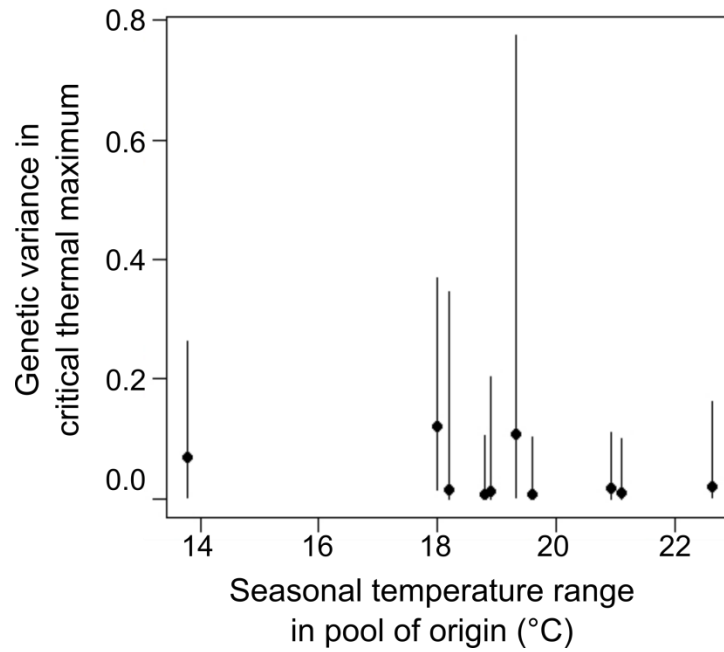


Figure 4. Estimates of genetic variation in critical thermal maximum of *Daphnia magna* sampled from 10 different pools versus the seasonal temperature range in each pool. Points are the median estimate in each of the 10 pools and error bars are 95% credible intervals from a Bayesian mixed-effects model.

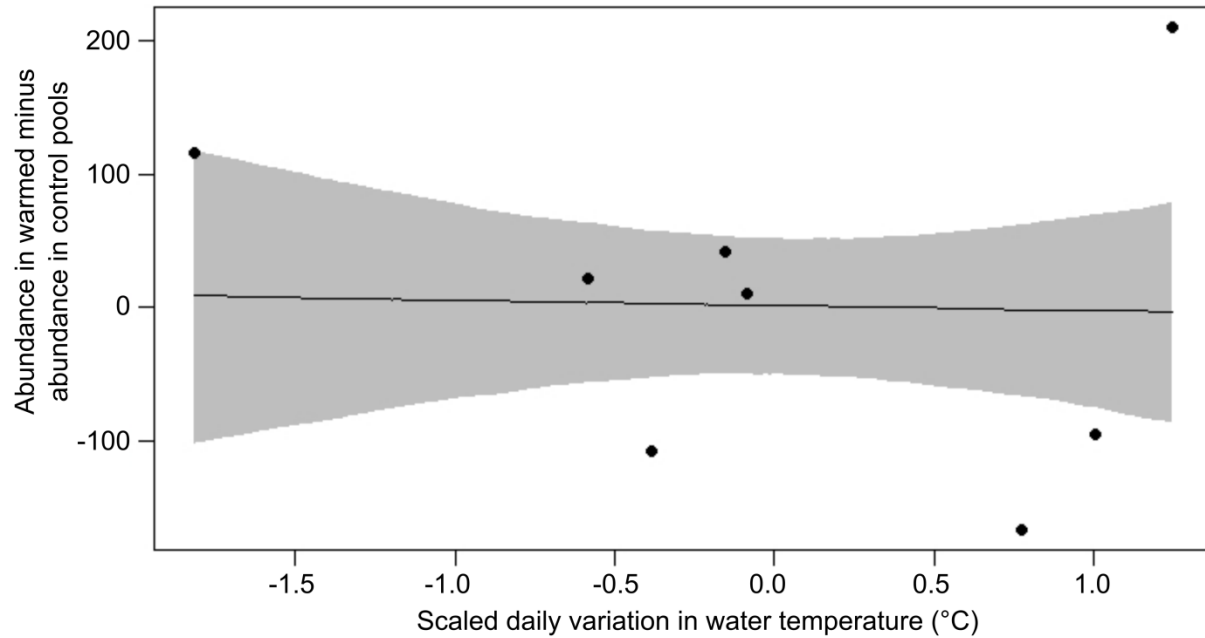


Figure 5. The difference in *Daphnia magna* abundance between control and warmed artificial pools does not depend on temperature variation in the natural pool of origin. We seeded each pair of artificial pools with a genetically identical mixture of 40 *D. magna* neonates from a single natural pool. Natural pools differed in the degree of temperature variation (x-axis). Temperature variation on the x-axis is mean centered and standardized to have an SD equal to 1. The horizontal line and shaded area indicate the slope and 95% CI of the relationship between the difference in abundance and the temperature variation in the pool of origin as estimated from a Bayesian linear model.

SUPPLEMENTAL MATERIAL

Re-analysis Excluding Pools with High Clonal Loss:

We reanalyzed the data including only data from clones collected in 2018 and only pools where ≥ 14 clones survived in the lab (i.e., pools 1, 2, 8, 9, 10; Table S1) to determine if the loss of clones in the lab affected our conclusions. We removed the year fixed effect from all models because the data only included clones collected in 2018. Otherwise, the analysis remained the same as described in the methods.

When *D. magna* developed at 20°C, the top model (M1-1) received 65.3% of the stacking weight and included genetic variation in CTmax, but no microgeographic adaptation or differences in genetic variation among pools (Table S2). The percent of phenotypic variation explained by differences among clones (i.e., heritability) from this model was 25.7% (95% CI = 5.9% – 44.7%). The remaining models received $\leq 27.0\%$ of the stacking weight. Hence, as we did in the full-data analysis, we concluded that there is genetic variation in CTmax in the metapopulation, but genetic variation is not maintained by differences in temperature variation among pools as predicted.

When *D. magna* developed at 25°C, the top model (M1-2) received 56.3% of the stacking weight and included differences in average CTmax among pools. However, the pool effects were small and driven mostly by the coldest pool (Fig. S1). Moreover, the model predicted that individuals from the coldest pool had the highest CTmax, which is opposite of our prediction (Fig. S2). Similar to the full-data analysis, the model suggesting there was no genetic variation among clones (M1-0) received 43.7% of the stacking weight. Further supporting this model, estimates of heritability from model M1-1 were 89% lower relative to heritability estimates from *D. magna* that developed at 20°C (median heritability = 2.8%, 95% CI = 0.3% – 16.8%). Hence,

as we did in the full-data analysis, we concluded there was little or no genetic variation in CTmax when individuals developed at 25°C.

The top model from the suite of models used to evaluate plasticity (M2-1) received 48.6% of the stacking weight (Table S3) and suggested there was plasticity in CTmax, but no genetic variation in plasticity. The model suggesting plasticity differed depending on the of pool temperature predictability (M2-3) received 37.4% of the stacking weight. However, the 95% credible interval of the interaction term describing the relationship between plasticity and the predictability of pool temperature overlapped zero (95% CI of interaction = -0.241 – 0.930), which suggests no strong relationship. The remaining models each received $\leq 14.0\%$ of the stacking weight. Hence, we conclude there is plasticity in CTmax, but no microgeographic adaptation in CTmax plasticity, as we did in the full-data analysis.

Table S1. The number clones included in the analysis from each pool and year. In 2018, we collected 25 clones from each pool. However, some clones died or produced males in the lab, which ended their clonal line before we measured CTmax. Average maximum temperature is the average maximum temperature during August 2018.

Pool	2017	2018	Average Maximum Temperature
1	0	18	23.7
2	0	19	24.7
3	6	0	25.4
4	7	6	25.7
5	2	7	26.1
6	1	7	26.2
7	7	0	26.8
8	0	14	27.0
9	1	22	28.0
10	0	14	28.1

Table S2. Model comparison to evaluate whether there is genetic variation in the critical thermal maximum (CT_{max}) of *Daphnia magna*, whether genetic variation stems from microgeographic adaptation, and whether the results differ depending on the developmental temperature (20°C or 25°C). In this analysis, we only included clones collected in 2018 from pools where at least 14 clones survived in the lab (i.e., pools 1, 2, 8, 9, 10; Table S1). We used approximate leave-one-out cross validation and Bayesian stacking weights for model comparison. P_{eff} is the effective number of parameters, ELPD is the expected log predictive density, ΔELPD is the difference in ELPD from the top model, and $\Delta\text{ELPD SE}$ is the standard error in ΔELPD . In the Model column, parameters expressed as (1|x) are random intercept terms, year is the year of the experiment (2017 or 2018), pool is the natural pool of origin, max_temp is the maximum temperature in the pool of origin, and (1|clone_p) is a random effect where the variance among clones (i.e., the genetic variation) is allowed to vary among pools. All models also included a random intercept for the CT_{max} trial, which is not shown.

Hypothesis	Model	P_{eff}	ELPD	ΔELPD	$\Delta\text{ELPD SE}$	Stacking Weight
20°C						
M1-1: Genetic var.	CT _{max} ~ year + (1 clone)	47.0	-137.9	0.0	0.0	0.653
M1-4: Genetic var. differs among pools	CT _{max} ~ year + (1 clone _p)	43.9	-138.3	-0.4	1.9	0.270
M1-0: No genetic var.	CT _{max} ~ year	18.5	-145.5	-7.6	4.3	0.077
M1-3: Microgeographic adaptation	CT _{max} ~ year + max_temp + (1 pool) + (1 clone)	48.3	-139.4	-1.5	1.0	0.000
M1-2: Microgeographic adaptation	CT _{max} ~ year + pool + (1 clone)	49.1	-140.6	-2.7	1.4	0.000
25°C						
M1-2: Microgeographic adaptation	CT _{max} ~ year + pool + (1 clone)	25.3	-128.9	-0.2	1.0	0.563
M1-0: No genetic var.	CT _{max} ~ year	16.4	-129.6	-0.8	2.7	0.437
M1-3: Microgeographic adaptation	CT _{max} ~ year + max_temp + (1 pool) + (1 clone)	24.4	-128.7	0.0	0.0	0.000
M1-1: Genetic var.	CT _{max} ~ year + (1 clone)	22.5	-129.5	-0.7	2.5	0.000
M1-4: Genetic var. differs among pools	CT _{max} ~ year + (1 clone _p)	31.1	-129.7	-0.9	2.3	0.000

Table S3. Model comparison to evaluate whether there is plasticity in the critical thermal maximum (CTmax) of *Daphnia magna*, genetic variation in that plasticity, and microgeographic adaptation. In this analysis, we only included clones collected in 2018 from pools where at least 14 clones survived in the lab (i.e., pools 1, 2, 8, 9, 10; Table S1). We used approximate leave-one-out cross validation and Bayesian stacking weights for model comparison. P_{eff} is the effective number of parameters, ELPD is the expected log predictive density, ΔELPD is the difference in ELPD from the top model, and $\Delta\text{ELPD SE}$ is the standard error in ΔELPD . In the Model column, year is the year of the experiment (2017 or 2018), dev_temp is the developmental temperature (20°C or 25°C), pool is the natural pool of origin, pool_temp_SD is the daily variation in maximum temperature, and pool_temp_pred is the predictability of daily temperature variation. Parameters expressed as (y|x) are random slope terms where the slope for y varies among levels of x. Parameters expressed as (1|x) are random intercept terms. All models also included a random intercept for the CTmax trial, which is not shown.

Hypothesis	Model	P_{eff}	ELPD	ΔELPD	$\Delta\text{ELPD SE}$	Stacking Weight
M2-1: Plasticity	CTmax ~ year + dev_temp + (1 clone)	48.1	-265.1	0.0	0.0	0.486
M2-5: Microgeographic adaptation	CTmax ~ year + dev_temp * pool_temp_pred + (dev_temp clone) + (1 pool)	54.3	-265.5	-0.5	2.8	0.374
M2-0: No plasticity	CTmax ~ year + (1 clone)	45.4	-283.1	-18.0	7.2	0.140
M2-2: Genetic var. in plasticity	CTmax ~ year + dev_temp + (dev_temp clone)	54.9	-265.8	-0.8	0.9	0.000
M2-4: Microgeographic adaptation	CTmax ~ year + dev_temp * pool_temp_SD + (dev_temp clone) + (1 pool)	54.5	-266.1	-1.1	2.7	0.000
M2-3: Microgeographic adaptation	CTmax ~ year + dev_temp * pool + (dev_temp clone)	55.8	-266.6	-1.5	2.6	0.000

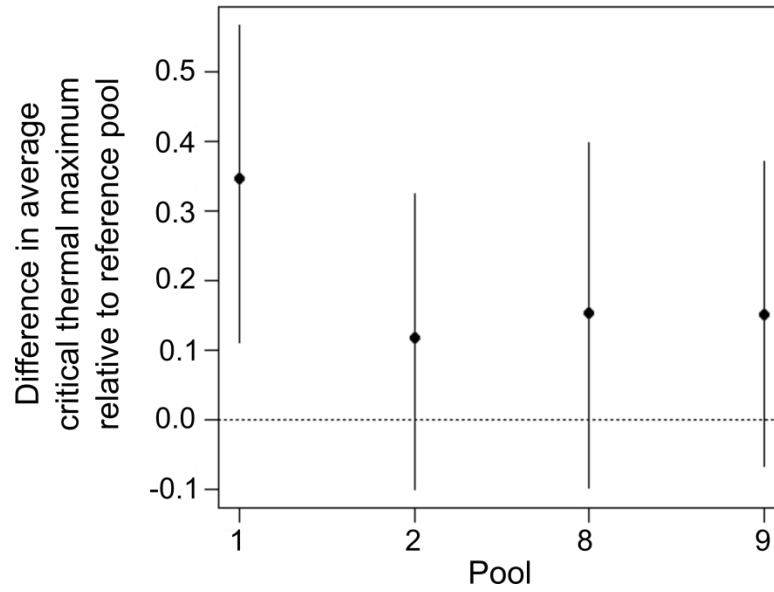


Figure S1. Differences in average critical thermal maximum (°C) of *Daphnia magna* from four pools relative to a reference pool (pool 10). In this analysis, we only included clones collected in 2018 from pools where at least 14 clones survived in the lab (i.e., pools 1, 2, 8, 9, 10; Table S1). Points are the median estimate in each of the five pools and error bars are 95% credible intervals from a Bayesian hierarchical model. Pools are ordered from the coolest (left) to the warmest (right) maximum temperature (Table S1).

Chapter 4: Fine-scale Refugia Conserve Regional Biodiversity Under Climate Change

ABSTRACT

Climate change is affecting biodiversity around the globe in predictable ways, ranging from poleward shifts in species distributions to an increase in warm-adapted species in local communities (i.e., thermophilization). However, these impacts are not occurring homogeneously around the globe, and observed biodiversity impacts are often opposite of those predicted based on changes in temperature. Microclimates, which are often overlooked in climate change biology, could explain why observed biodiversity impacts vary among locations and often differ from predictions. Here, we map microclimates in freshwater rock pools and evaluate how microclimates alter predictions of climate change impacts on biodiversity. We demonstrate that temperatures can differ substantially (8 – 9°C) among pools less than a meter apart. We then show that these microclimates significantly alter predictions of climate change impacts on biodiversity. Macroclimate predictions, which ignore microclimates, predict low future occupancy (3 – 9%) and persistence probability (<1 - 31%) for cold-adapted organisms in our study area, and therefore predict decreases in gamma diversity from 13 to 11 organisms and substantial thermophilization. However, predictions incorporating microclimates suggest cool locations will remain suitable for cold-adapted organisms in the future. Therefore, predictions including microclimates suggest no change in gamma diversity and an 80% decrease in thermophilization. Cool locations reduce the impacts of climate change because they are colder than the surrounding microclimates, but also because they warm less than warmer microclimates. Cool microclimates are also predicted to become suitable for warm-adapted organisms under climate change, which has important conservation implications. Our models suggest that

protecting just the 10 coolest rock pools (representing 9% of locations on the landscape) results in a 97 – 100% chance of conserving all focal organisms in the future. In contrast, protecting the 10 currently most biodiverse pools results in just a 1 - 33% chance of conserving all focal organisms in the future. Our results therefore suggest that we must account for microclimates if we hope to make accurate predictions of future climate change impacts and that currently cool microclimates could be an efficient tool to conserve regional biodiversity.

INTRODUCTION

Forty-years ago, biologists predicted that human-induced climate change would have significant effects on biodiversity around the globe (McLean 1978, Peters and Darling 1985, Peters and Lovejoy 1994, Urban 2019). Since that time, the burgeoning field of climate change biology has documented clear fingerprints of climate change (Parmesan and Yohe 2003, Root et al. 2003, Scheffers et al. 2016). Many species are shifting their distributions poleward and up in elevation to track suitable climates (Chen et al. 2011, Freeman et al. 2018). Species are also adapting *in situ* by adjusting the timing of key life events (Parmesan and Yohe 2003, Root et al. 2003, Scheffers et al. 2016), reducing their body size (Gardner et al. 2011, Sheridan and Bickford 2011), or evolving new climatic tolerances (Geerts et al. 2015). The fingerprints of climate change are also notable at a community scale. The loss of cold-adapted species and gain of warm-adapted species in many locations is resulting in a shift toward warm-adapted communities (i.e., thermophilization; De Frenne et al. 2013, Duque et al. 2015). The magnitude of these climate change responses is often associated with the magnitude of climate change in a region, which provides compelling evidence that climate change is indeed the mechanism driving the observed changes (Root et al. 2003, Chen et al. 2011, De Frenne et al. 2013).

However, these fingerprints of climate change are not occurring homogeneously around the globe and regional differences in temperature change explain only a small proportion of variation in climate change responses. For instance, the magnitude of temperature change only explains 34.8% and 13.7% of the variation in latitudinal and elevational range shifts (respectively) based on a meta-analysis of 1367 species responses (Chen et al. 2011). Moreover, 22% and 25% of species in that meta-analysis shifted their distribution towards the equator or down in elevation, in opposition to the predicted responses based on warming (Chen et al. 2011). Similarly, *in-situ* and community responses to climate change differ among locations and are not always in the direction expected based on warming (Primack et al. 2009, Gardner et al. 2011, De Frenne et al. 2013, Rafferty et al. 2020). Explaining why climate change responses vary among locations could improve future predictions of climate change impacts. Moreover, explaining variation in climate change responses could help determine where species might be resilient to climate change and therefore help design strategies to minimize future biodiversity loss. Hence, understanding spatial variation in climate change responses is a next big challenge in climate change biology.

Microclimate variation, although often overlooked in climate change biology, could explain substantial variation in climate change responses (Lenoir et al. 2017, Nadeau et al. 2017a). Microclimates can affect the response of species to climate change in three key ways. First, species that occur in areas with high microclimate variation might often have broader climatic tolerances, which makes them less sensitive to climate change (Bonebrake and Deutsch 2012). Second, species that occur in landscapes with high microclimate variation might need to move just a short distance to track suitable climates, therefore alleviating the need for *in-situ* adaptation or longer-distance range shifts (Loarie et al. 2009). For example, Scheffers (2013)

predicts that many anuran species will move from warm rainforest canopies toward cooler ground environments as climates change. Third, microclimates can act as refugia where species can persist for many generations, despite unfavorable changes in climate at larger spatial scales (Morelli et al. 2016). Microclimate refugia likely helped species persist through past climate changes (Rull 2009, de Lafontaine et al. 2014, Patsiou et al. 2014) and are currently reducing local extirpations in coastal grassland plants in the United Kingdom (Maclean et al. 2015). For these reasons, microclimates and microclimate variation might often buffer species from the effects of climate change at larger spatial scales and result in unexpected climate change responses (De Frenne et al. 2013, Patsiou et al. 2014, Maclean et al. 2015, Lenoir et al. 2017, Suggitt et al. 2018). Moreover, the potential buffering capacity of microclimates could make them an efficient means of conserving biodiversity in some areas (Groves et al. 2012, Nadeau and Fuller 2016).

Despite their potential importance, most studies in climate change biology overlook microclimates by using climate data with a coarse spatial resolution (Potter et al. 2013, Nadeau et al. 2017b). For example, Potter (2013) showed that models to predict future species distributions use climate data with a spatial resolution that is 10,000- and 1000-fold larger than the body size of focal animals and plants, respectively. Scaling climate data to the body size of focal species may not be necessary to understand climate change responses (Bennie et al. 2014). However, the spatial resolution of climate data is often orders of magnitude too coarse even when it is compared to the area that encompasses a population of the focal species (Nadeau et al. 2017b). Using these coarse-resolution data masks the buffering potential of microclimates, which can result in significantly different expectations of how biodiversity will respond to climate

change (Luoto and Heikkinen 2008, Randin et al. 2009, Gillingham et al. 2012, Franklin et al. 2013, Slavich et al. 2014, Lenoir et al. 2017).

Although climate scientists and climate change biologists are rapidly producing climate data at finer spatial resolutions (Bramer et al. 2018, Zellweger et al. 2019, Kearney et al. 2020, Maclean 2020), incorporating microclimates into predictions of species climate change responses is still in its infancy and many important questions remain (Lenoir et al. 2017, Lembrechts et al. 2019, Zellweger et al. 2019). First, most approaches to mapping microclimates, and most studies incorporating microclimates in climate change biology, focus on the effects of topography (e.g., elevation, slope, aspect; Lenoir et al. 2017). However, many other factors such as soil moisture and forest-canopy density can affect microclimates (Bramer et al. 2018), and microclimate variation can be large even in topographically homogenous landscapes (Milling et al. 2018). Second, unlike topographic effects, many non-topographic effects might be altered by climate change therefore altering future microclimates (Bramer et al. 2018), a topic in need of much further study (Lenoir et al. 2017, Davis et al. 2019, Zellweger et al. 2019). Last, microclimates can reduce the effects of climate change by remaining suitable despite experiencing the same level of climate change as surrounding areas (i.e., buffering) or because microclimates are less affected by climate change relative to surrounding areas (i.e., decoupling) (Gollan et al. 2014, Lenoir et al. 2017). Few studies have accounted for the potential of decoupling, and only one simulation study has evaluated the relative benefits of decoupling and buffering effects on biodiversity under climate change (Lenoir et al. 2017). These questions remain unanswered due to their complexity and the detailed data required to model all the factors potentially affecting microclimates (Lenoir et al. 2017). Hence, studying a system where we can accurately model microclimates, how microclimates might change over time, and how they alter the fingerprints of

climate change could provide significant insight into where and why climate change will have the greatest impacts.

Here, we develop hydrologic and water-temperature models to map microclimates at a sub-meter resolution in freshwater rock pools (Brendonck et al. 2010, Jocque et al. 2010). Freshwater rock pools are small depressions in bedrock that fill with rainwater. In our study area, rock pools occur in a landscape with little topographic variation and no vegetation. Nevertheless, temperatures in rock pools less than a meter apart can differ substantially due to differences in water depth and micro-topographic (e.g., boulders, crevices) effects on solar exposure. Moreover, we can predict how those factors will change in the future with high accuracy. We use maps of microclimate variation to estimate occupancy-habitat relationships for 13 organisms that currently occur in our study area and predict how changes in hydrology, temperature, and microclimate variation will alter biodiversity in the future. We compare predictions of the impacts of climate change on biodiversity using macroclimate data, microclimate data without decoupling (i.e., all locations warm equally), and microclimate data including decoupling (i.e., differential warming among locations) to better understand how microclimates affect the fingerprints of climate change. Last, we evaluate how biodiversity might reshuffle among the microclimates within our study area and test the value of cooler microclimates for conserving current biodiversity relative to another common conservation strategy. Our research in this tractable model system provides unique insights into the importance of microclimates and how microclimates reduce the impacts of climate change on biodiversity.

METHODS

Study System:

We mapped microclimates and predicted climate change impacts in 149 freshwater rock pools that occur in a 1.9 ha study area on Schoodic Point in Acadia National Park, Maine, USA (Fig. S1). The freshwater rock pools on Schoodic Point occur on exposed bedrock on the coast between the intertidal and the forest edge. Pools in our study area range in size from 0.07 – 71.52 m² and vary between 7.0 and 55.5 cm in maximum depth. Coastal winds regularly mix the water and therefore temperature is often homogenous throughout the water column within a pool. The fate of future microclimates will likely depend on the effect of climate change on water depth. For example, cooler microclimates could disappear if increased evaporation and decreased rainfall result in significant decreases in water depth. Fortunately, water depth can be modeled accurately in freshwater rock pools with a simple hydrologic model because there is no vegetation and no groundwater influences (Vanschoenwinkel et al. 2009, Tuytens et al. 2014). Hence, it is not only possible to predict fine-scale variation in microclimates, it is also possible to predict how microclimate variation might change in the future.

Climate Data:

We used data from two weather stations to develop and test hydrologic and water-temperature models: (1) the weather station at the Schoodic Education and Research Center located ~250 m from our study site (SERC), and (2) the Acadia National Park Global Historical Climatology Network station located ~14 km from our study site (ANP). Daily data from the SERC station was available for the period 2013 - 2018 and included minimum, maximum, and average temperature, minimum and maximum humidity, total precipitation, and average wind

speed. We used daily data between 1989 – 2012 from the ANP station, which included minimum and maximum temperature, and total precipitation.

We also used daily outputs from four earth systems models included in the fifth Coupled Model Intercomparison Project to predict the impacts of climate change on hydrology and water temperature in each pool. The models included: (1) The Australian Community Climate and Earth System Simulator coupled model (ACCESS; Bi et al. 2013), (2) The Canadian Earth System Model (CanESM2; Chylek et al. 2011), and two variants of the Geophysical Fluid Dynamics Laboratory’s Earth Systems Model - (3) ESM2G (GFDL-ESM2G) and (4) ESM2M (GFDL-ESM2M) - which differ in their physical ocean component (Dunne et al. 2012). This suite of models represents a wide range of future climate conditions in our study area (Fig. S2). We bias corrected the output for these models to represent the climates on Schoodic Point using a combination of daily weather data from the SERC and ANP weather stations. We used only data from the SERC weather station to bias correct precipitation, humidity, and wind speed because data from the ANP station were unavailable for these variables. We used empirical quantile mapping with the R package ‘*qmap*’ to correct biases in the data. We used a bootstrap with 1000 replicates to estimate the empirical quantiles. We bias corrected daily model outputs from a 30-year current (1989 - 2018) and future period (2071 - 2100) that assumes high future greenhouse-gas emissions (RCP 8.5).

Rock Pool Hydrology:

We modified the water-balance model described by Vanschoenwinkel et al. (2009) to model current and future daily water depths in each focal pool. The model (Eq. 1) describes water depth ($D_{p,t}$) in each pool p on day t as a function of water depth on the previous day ($D_{p,t-1}$), daily evaporation (E_t), a pool-specific overflow amount ($O_{p,t}$), daily precipitation (P_t),

and a catchment factor (R). The catchment factor relates the amount of daily precipitation to the change in water depth in each pool by accounting for runoff.

$$D_{p,t} = D_{p,t-1} + (P_t * R) - E_t - O_{p,t} \quad \text{Eq. 1}$$

We predicted daily evaporation using the Penman Equations (Penman and Keen 1948) in the R package ‘*Evapotranspiration*’. These equations predict the amount of daily evaporation using day length, average daily wind speed, and the daily minimum and maximum air temperature and humidity. We calculated overflow for each pool and day as $O_{p,t} = D_{p,max} - D_{p,t}$, where $D_{p,max}$ is the maximum depth in each pool. We determined the maximum water depth in each pool by measuring the depth in the deepest part of the pool the day after a heavy rain. We estimated the catchment factor using daily water-depth data from data loggers (model: Onset Hobo U20L) deployed in 13 pools in 2017 and 2018. We used this data to estimate the catchment factor using a linear mixed effects model with change in water depth ($D_{p,t} - D_{p,t-1}$) as the response variable, daily precipitation as the independent variable, and pool as a random factor. We restricted the data for this regression to days when the amount of precipitation was > 0 and ≤ 5 mm to limit the potential effects of overflow on the estimates of catchment factor. This regression suggested that on average 1 mm of rain causes an 8.4 mm (SE = 0.98) increase in water depth. Hence we used $R = 8.4$ mm for each pool in the model.

We evaluated the hydrologic model by comparing predictions of daily water depth to data from the water-depth data loggers described above. We predicted the water depth in 2017 (five pools) and 2018 (nine pools) starting at the maximum depth for each pool on April 1 and ending on November 31. Pools are often at their maximum depth in early April due to high spring precipitation and snowmelt and often freeze in late November. We used daily weather data from the SERC weather station to predict daily evaporation.

Last, we used the methods described above to predict daily water depth in each pool between April and November using weather predictions from the four climate models described above for each day of the 30-year current and future period. We used these predictions to evaluate whether climate change would alter the average hydroperiod across pools. Hydroperiod – defined here as the maximum number of consecutive days when the water depth was >25 mm in a pool – is one of the most important variables explaining biodiversity in freshwater rock pools (Jocque et al. 2010). We used a paired Wilcoxon signed rank test to compare the average hydroperiod between the current and future period.

Water Temperature:

We used statistical models to estimate current water temperatures and predict future water temperatures for each pool in the study area. We based the statistical models on hourly water temperature data measured with temperature data loggers (models: HOBO Pendant UA-001-08 or Onset Hobo U20L) placed in 40 different pools between 2016 and 2018. We placed water-temperature data loggers in the deepest part of the pool and covered them with a rock to shade them from direct sunlight. We used the hourly water temperature data to determine the maximum daily water temperature in each pool, resulting in a total of 7798 daily measurements of minimum and maximum water temperature.

We used generalized additive models in the R package ‘*mgcv*’ to predict current and future water temperatures in all pools. Generalized additive models allow for nonlinear relationships between predictor variables and water temperature. For example, other studies have identified an s-shaped relationship between air and water temperature due to the effects of freezing and evaporative cooling (Mohseni et al. 1998, Morrill et al. 2005, Harvey et al. 2011). We modeled daily maximum water temperature using the following daily covariates: minimum

water temperature, maximum air temperature from the SERC weather station, solar radiation, the amount of precipitation from the SERC weather station, and depth. We also allowed the effect of air temperature and solar radiation to vary depending on depth and the effect of solar radiation to vary depending on the amount of precipitation, which we assume is a proxy for cloudiness. We modeled daily minimum water temperature using the following daily covariates: maximum water temperature on the previous day, minimum air temperature from the SERC weather station, depth, and an interaction between depth and air temperature. We included pool as a random effect in all models to account for the correlation among measurements within a pool. We measured daily solar radiation using CIMES-FISHEYE, which is a program to estimate forest canopy geometry and solar radiation from hemispherical photographs. We took hemispherical photographs with a hemispherical camera (Kodak PixPro SP360) floating on the surface in the center of each pool. We used estimates of daily total photosynthetically active radiation from CIMES-FISHEYE given clear skies as a proxy for daily total solar radiation in each pool. We estimated the daily water depth in each pool using the hydrologic model described above.

We evaluated the model by predicting daily maximum and minimum water temperature in 10 randomly selected pools that were not included in the model development above, which included 2027 measurements of minimum and maximum water temperature. We predicted the minimum and maximum water temperature in each pool sequentially starting on April 1 and ending on November 31 of each year, regardless of the observation period in each pool. We used this method because the model for maximum water temperature depends on minimum water temperature on the same day, and the model for minimum water temperature depends on the maximum water temperature of the previous day. We set the maximum and minimum water temperature on April 1 to the maximum and minimum observed air temperature during that day.

We then looped through the days and used the statistical models described above to predict minimum and then maximum water temperature on each day in each of the three years. We compared the water temperature predictions to observed water temperatures in the pool each day.

Last, we used the methods above to predict minimum and maximum water temperature for each pool using climate data from the four climate models described above for each day of the current and future period. We focus our results on changes in maximum water temperature because maximum and minimum water temperatures are correlated and we use average maximum water temperature to predict the impacts of climate change on biodiversity.

Habitat Associations of Focal Organisms:

We sampled invertebrates from 107 rock pools in the study area in May and August of 2017 using either a dip net (in pools with a surface area $< 8 \text{ m}^2$) or a plankton tow. We soaked nets in 10% bleach and rinsed them thoroughly offsite between samples to prevent cross-contamination of pools or samples. We sampled each pool thoroughly; however, we also collected two samples from six pools in May and 12 pools in August to provide survey replication in addition to the replication between months. We also recorded the presence of organisms observed in the pool, but not captured during sampling. We emptied samples from nets into a white tub and recorded all organisms present to the taxonomic levels defined in Table S1. We then preserved the samples in 70% ethanol. We identified organisms using a microscope (Leica M125, Leica Microsystems, Germany) in the lab for 48 samples, which confirmed the accuracy of our field identifications and allowed us to detect microscopic organisms that we were unable to observe in the field (Table S1). We identified larval aquatic insects following Peckarsky et al. (1990) and all other organisms following Aliberti et al. (2013).

We used a Bayesian multi-species occupancy model (MSOM) to estimate the habitat associations of each organism and predict the effects of climate change. An MSOM estimates species-habitat relationships while accounting for the fact that some species may be present, but undetected during sampling (Dorazio and Royle 2005, Royle and Dorazio 2009). Preliminary analyses demonstrated habitat estimates were highly uncertain for organisms detected in fewer than 10 pools. We therefore restricted our data to include only organisms we observed in at least 10 pools during sampling, resulting in a total of 13 organisms included in the model (Table S1). Initially, we included the following environmental variables in the model to explain occupancy of each organism: dissolved organic carbon, conductivity, pH, average maximum temperature, and average maximum hydroperiod. These variables are known to affect rock pool biodiversity in many other freshwater rock pool ecosystems, including a similar rock-pool metacommunity on a nearby island (Jocque et al. 2010, Simonis and Ellis 2014). We estimated average maximum temperature and hydroperiod using the models described above and climate data from the SERC weather station between 2013 and 2017. We used the average pH and conductivity measurements taken in each pool in May and August 2017. We measured dissolved organic carbon from water samples collected in August 2017 using fluorometry. We also included a variable indicating whether we processed the sample with a microscope, the net-type (dip net or plankton tow), the sample volume (i.e., the length of the sample times the area of the net), and the month of the sample (May or August) as factors affecting the detection probability of each organism. The 95% credible interval of the coefficient for conductivity, pH, hydroperiod, net type, and sample volume overlapped zero for all organisms. We therefore removed these variables from the final model.

We fit the model using Monte Carlo Markov Chain (MCMC) estimation in JAGS using the ‘*R2jags*’ package in R version 3.6.0. We used normal priors with a mean equal to zero and precision equal to 0.001 for all mean hyperparameters, and a uniform distribution between zero and one for the variance hyperparameters. We ran three chains for 75,000 iterations with a burn-in period of 15,000 and saved every fiftieth draw, resulting in 3600 posterior samples. All parameters had a Gelman-Rubin statistic <1.1 , suggesting the chains converged (Gelman and Hill 2006). We evaluated the model using area under the receiver operating characteristic curve (AUC) following methods described by Zipkin et al. (2012) for AUC estimation given imperfect detection. AUC values range between zero and one, and models with a value above 0.7 are considered to have decent predictive ability (Zipkin et al. 2012). Applying AUC to an MSOM provides an overall estimate of the predictive ability across all organisms and estimates for each organism.

Current and Future Biodiversity Predictions:

We used the MSOM to generate posterior predictions of occupancy probability for each organism based on predicted average conditions in the current (1981 – 2018) and future (2071 – 2100) period for each of the four climate models. We made predictions using both the average maximum water temperature across all pools (hereafter macroclimate predictions) and the average maximum water temperature predicted for each of the 107 pools (hereafter microclimate predictions). We further separated microclimate predictions into predictions with buffering only (i.e., all pools warm the same amount) and predictions including buffering and decoupling (i.e., differential warming among pools). To generate microclimate predictions with buffering only, we simulated data where all pools warmed by the maximum amount of warming predicted for any pool under each climate change model. We assumed all other environmental variables

remained constant between the two periods and used the mean values across pools for the macroclimate predictions. We converted all the posterior predictions of occupancy probability to presence/absence data using the observed prevalence (i.e., the proportion of sites where we observed each organism) as a threshold to convert occupancy probability to presence/absence data (Liu et al. 2005, Jiménez-Valverde and Lobo 2007). We considered a site occupied by an organism if the estimated occupancy probability at a site was greater than or equal to the observed prevalence of that organism. This threshold approach produced very similar results to a non-threshold approach. Hence, we present the threshold approach here and the non-threshold approach in the supplement.

We compared four measures of climate change impacts among the macro and microclimate predictions to determine the effect of microclimates and the effect of buffering versus decoupling. First, we compared the future occupancy probability for cold-adapted organisms among the macro and microclimate predictions. We assumed organisms were cold adapted if the 97.5% quantile of their occupancy-temperature relationship from the MSOM was less than zero. For the microclimate predictions, we used the maximum occupancy probability among the 107 pools. Second, we compared the future persistence probability for the cold-adapted organisms. We estimated persistence probability as the proportion of posterior predictions that predicted the organism present in the study area. Third, we compared the number of currently occurring organisms predicted to occur in the study area in the future (gamma diversity). Last, we compared a measure of thermophilization between the macro and microclimate predictions. We estimated thermophilization as the change in the community temperature index (CTI) between the current and future period (Devictor et al. 2008). We

estimated the community temperature index (CTI) as the weighted mean temperature preference of each organism in the community as follows:

$$CTI = \frac{1}{13} \sum_{s=1}^{13} \Psi_s * \beta_{temp,s}$$

where Ψ is the occupancy probability for organism s in the community and β_{temp} is the occupancy–temperature relationship identified from the MSOM for organism s . For the microclimate predictions, we used the maximum value of Ψ_s from the 107 pools. Positive values of CTI suggest the community is dominated by organisms with a positive occupancy-temperature relationship and vice versa. Positive values of thermophilization suggest a predicted increase in warm-adapted organisms or a loss of cold-adapted organisms in the community in the future. This measure of thermophilization is also a method of estimating community change that incorporates uncertainty in the estimates of occupancy probability and does not require us to convert estimates of occupancy probability to presence/absence data.

We also used the posterior predictions from the microclimate data to evaluate how biodiversity might reshuffle among the rock pools within the study area, which provides insights into future conservation strategies. Specifically, we evaluate how changes in alpha diversity and community composition between the current and future period differ among microclimates. We also used the posterior predictions of presence/absence in each pool to evaluate two conservation strategies: (1) conserving the 10 currently most biodiverse pools, and (2) conserving the 10 pools with the coolest microclimates. We used the probability of conserving all 13 organisms as the outcome to compare the two conservation strategies, which assumes the conservation objective is to maintain current biodiversity. Conserving the most diverse locations in a landscape is a

common conservation strategy worldwide. Conserving cooler microclimates is increasingly recommended as a biodiversity conservation strategy under climate change.

Evaluating Statistical Predictions:

Statistical predictions of species climate change responses are regularly criticized for ignoring the potential that extreme temperatures will exceed species climatic tolerances, for ignoring the potential for species interactions, and for assuming unlimited dispersal and access to newly suitable locations (Hampe 2004, Heikkinen et al. 2006, Urban et al. 2016). One advantage of working in a tractable model system is that we can evaluate some of these assumptions using lab and field experiments.

We used lab experiments to measure the critical thermal maximum (an estimate of upper temperature tolerance) for a subset of our focal organisms. Critical thermal maximum estimates allowed us to determine if extreme temperatures are likely to exceed the temperature tolerances of focal organisms in each pool and evaluate if cool pools will provide a refuge for cold-adapted organisms. We measured critical thermal maximum on the following organisms that we collected from 10 pools in 2017 (see Table S1 for further taxonomic information): *Daphnia magna* (N = 17), *Ceriodaphnia dubia* (N = 16), Calanoid copepods (N = 9), predacious diving beetles (N = 8), water boatman (N = 16), mosquito larvae (N = 6), and chironomids (N = 8). We kept organisms at ambient air temperature for 24 hours and then in the lab at 20°C for an additional 24 hours to provide a common acclimation environment. We then put individuals of each organism in separate 5 ml glass beakers filled with water. We placed the beakers (20 per trial) in a water bath set to ~25°C and raised the temperature by 0.5°C per minute. We recorded the temperature at which each individual stopped swimming and either sank to the bottom or floated to the top. We used the critical thermal maximum data to evaluate the number of years in which

maximum annual temperatures in each pool exceeded the critical thermal maximum of each organism.

We also used a whole-ecosystem warming experiment in artificial rock pools (Fig. S3) to evaluate our statistical predictions, to test if focal organisms colonize newly suitable habitat, and test if cold- and warm-adapted organisms could coexist. In early June 2017, we installed 10 groups of artificial pools with three treatments per group (30 pools total): (1) a control, (2) a warming treatment, and (3) a warming-plus-precipitation treatment. We fitted pools in both warming treatments with an open-top greenhouse (Fig. S3) that we constructed with 1-mm Sun-Lite® HP solar glazing (Solar Components Corporation). We created control pools similar to the warming treatment, but with mesh instead of plastic tops (Fig. S3), to control for possible effects of the top. In the warming-plus-precipitation treatment we also added rainwater periodically (see below) to simulate increased precipitation that is predicted by some climate models (Fig. S2). We collected rainwater onsite in plastic tubs and filtered it through 500- μ m mesh to remove invertebrates. We constructed artificial pools using 38 L plastic tubs (60 cm long, 40 cm wide, 22 cm deep) that we insulated with R-7.5 polystyrene rigid foam insulation and surrounded with large rocks to promote natural thermal inertia. We installed each group of artificial pools in the field next to a paired natural pool. We filled each artificial pool with 24 L of water from one of three large natural pools on site that we filtered through 500- μ m mesh to remove invertebrates. We put a temperature data logger in each pool and a water-depth data logger in two pools from each treatment, which recorded hourly water temperature and depth. We seeded each pool with invertebrates from the paired natural pool by first sampling invertebrates from the natural pool using a dip net, splitting the sample four ways using a plankton splitter, and putting 1/4 of the

sample in each artificial pool. Hence, each treatment within a natural-pool grouping started with very similar conditions.

After an initial 37 days, the warmed pools had significant water reductions because the greenhouses were blocking ~75% of precipitation. Hence, we modified the greenhouses to allow precipitation to runoff into the pools without affecting the temperature. We also added 2.8 L of water to the warmed treatment and 3.5 L to the warmed plus precipitation treatment to ameliorate the water-depth declines. We added more water to the warmed plus precipitation treatment to simulate higher precipitation. We sampled invertebrates in all pools in August 2017 using dip nets, preserved the samples in 70% ethanol, and determined the presence and absence of different organisms in the lab. Unfortunately, in the fall of 2017 the pools were destroyed by a coastal storm. Hence, our analysis is limited to the samples collected in August.

In early June 2018 we installed 16 redesigned artificial pools (eight controls and eight warmed) in two locations on Schoodic Point that were protected from storm activity (Fig. S3). We used larger 64 L (68 cm long, 46 cm wide, 32 cm deep) plastic tubs insulated with R-10 rigid foam insulation and surrounded each pool with large rocks inside and out to promote natural thermal inertia. We also redesigned the open-top greenhouses and screen tops to allow ~100% of precipitation to enter both control and warmed pools (Fig. S3). We filled the pools with 12 L of filtered water from each of three large pools (36 L total). We seeded each pair of artificial pools with *D. magna* neonates from one of eight natural pools. We obtained neonates by sampling 20 pregnant females from each natural pool and keeping them in captivity until they produced a brood. We then haphazardly selected four neonates from each female to put in the control and warmed pool (two neonates per pool, 40 neonates per pool total). We also added two ostracods from each of three natural pools (six total) to increase the reality of the community. We let other

organisms colonize the pools naturally, which provided a test of their colonization ability. We sampled invertebrates in each pool using a dip net in September 2018, 95 days after initiation. We preserved the samples in 70% ethanol and determined the presence and absence of the 13 focal organisms.

We evaluated whether the structure of rock pool communities differed among the treatments using a permutational multivariate analysis of variance (PERMANOVA). To analyze community structure, we first converted a site by community presence-absence matrix to a distance matrix using the '*vegdist*' function in the '*vegan*' package in R. We used the Jaccard index as a measure of distance among the communities. We then used PERMANOVA with the distance matrix as the response variable and treatment as the explanatory variable to evaluate whether community structure differed among the treatments. We used the '*adonis*' function from the '*vegan*' package to conduct the PERMANOVAs. We also used the '*simper*' function with 999 permutations to determine which organisms contributed to differences. SIMPER (similarity percentage) is a method to determine the average contribution of each organism to the dissimilarity among pairs of communities, where communities in this case are the treatments. We analyzed the 2017 and 2018 data separately. In the 2017 analysis, we included the natural-pool grouping as strata to constrain the permutations used to test for significance of the treatment effects. In the 2018 analysis, we used the location of the artificial pools as strata. We also quantified alpha richness in each pool and used a Friedman test (2017) or Wilcoxon signed-rank test (2018) to determine if alpha diversity differed among treatments.

RESULTS

Hydrology:

The mean error (i.e., estimated – observed depth) of water-depth predictions from our hydrologic model was 0.1 mm (SE = 0.7 mm) and the root-mean-squared error was 31.4 mm, suggesting that the predicted depths were unbiased and accurate. This error is within the typical error reported by the manufacturer for the water-depth data loggers (40 mm). Hence, we felt confident that the hydrologic model accurately represented rock pool hydrology. Our predictions suggest climate change will have minimal effects on rock pool hydrology. On average in the current period, we predict 71-75% (depending on the climate model) of pools remain inundated between April and November. In the future period, we predict 65-75% of pools will remain inundated between April and November. The average hydroperiod remained similar between the current and future periods, except for predictions from one climate model (Fig. 1A). Predictions from the CanESM model suggested the average hydroperiod across all pools will decrease by 10 days between the current and future period (Fig. 1A). The CanESM model predicts large temperature increases, decreases in humidity, and small decreases in summer precipitation (Fig. S2). The shortest hydroperiod we predicted was 42 days in the current period and 38 days in the future period, suggesting that hydroperiods are likely to remain similar in the future even in harsh years and in shallow pools.

Water Temperature:

The mean error for the test dataset from our water-temperature model was -0.2°C for minimum water temperature and -0.1°C for maximum water temperature, suggesting the estimates of water temperature were unbiased. The root-mean-squared error was 1.6°C for minimum temperature and 2.0°C for maximum temperature, suggesting some inaccuracy in the

estimates. However, these errors are similar to those reported in other studies using detailed models to predict temperature in microclimates (McCullough et al. 2016, Maclean et al. 2017, Meineri and Hylander 2017, Kearney et al. 2020, Maclean 2020). The errors are also small relative to the amount of temperature variation within and among pools. Water temperature can range 19°C in a day and 30°C in a year within a pool. Water temperature can also differ by as much as 15°C among pools within a day. Moreover, this error is less than the range of uncertainty in temperature change projections among climate models (Fig. S2).

Water temperatures differed substantially among pools due to differences in depth and solar exposure. Across climate models in the current period, the average maximum temperature in the warmest and coolest pools differed by an average of 8.1°C (SD among climate models = 0.02°C; Fig. 1B). On average across all pools, we predict average maximum temperature will increase between 1.9°C and 3.8°C, depending on the climate model (Fig. 1B). However, we predict cooler pools will warm less than warmer pools (i.e., cool pools have higher decoupling; Fig. 1B). For example, under the ACCESS climate model, we predict the warmest pool will warm 1.4°C more than the coolest pool in our study area (Fig. 1B). This difference in warming among the pools increases the difference in temperature between the warmest and coolest pools by 13% from 8.1°C to 9.2°C (SD = 0.34°C) on average across climate models in the future.

Statistical Biodiversity Predictions:

The median overall AUC value for our MSOM was 0.78, suggesting the model had acceptable predictive ability on average. *Daphnia magna* had the lowest median AUC value of 0.65 and non-biting midges (Family: *Chironomidae*) had the highest median AUC value of 0.89. The median AUC value for all other organisms was >0.70, suggesting the model performed well for most organisms on average. The MSOM identified two organisms with a negative

occupancy-temperature relationship (amphipods [Order: *Amphipoda*] and calanoid copepods [Order: *Calanoida*]; hereafter cold-adapted organisms) and three organisms with a positive occupancy-temperature relationship (ostracods [Order: *Podocopida*], mosquito larvae [*Aedes* sp.], and water boatman [*Trichocorixa verticalis*]; hereafter warm-adapted organisms; Fig. S4). Hence, we predict climate change will affect future occupancy for these five organisms. Three of these organisms also had a negative (amphipods and water boatman) or positive (mosquito larvae) occupancy-DOC relationship (Fig. S4). Therefore, DOC could constrain how these organisms respond to temperature changes in the future. For example, temperature may become suitable for an organism in the future, but occupancy probability could remain low if DOC is unsuitable.

Predictions among the climate models were quantitatively similar, hence we present predictions from the ACCESS climate model here, and results from the other climate models in the supplement (Figs. S4 and S5). Macroclimate predictions result in low occupancy probability for both cold-adapted organisms (Fig. 2A). The median occupancy probability from the macroclimate predictions was just 3% for amphipods and 9% for calanoid copepods in the future (Fig. 2A). Consequently, the predicted probability of future persistence in the study area is < 1% for amphipods and 31% for calanoid copepods (Fig. 2B), and therefore a median of only 11 organisms are predicted to persist in the future (Fig. 2C). Macroclimate predictions also suggest significant thermophilization due to decreases in the occupancy probability of cold-adapted organisms and increases in the occupancy probability of warm-adapted organisms (Fig. 2D). In contrast, the microclimate models that included both buffering and decoupling predict a median occupancy probability of 70% and 85% for amphipods and calanoid copepods respectively (Fig. 2A). Thus, microclimate models predict a 100% probability of persistence for both organisms

(Fig. 2B) and therefore predict all 13 organisms will persist in the community in the future (Fig. 2C). Microclimate predictions also predict an 80% reduction in median thermophilization (Fig. 2D).

Cool microclimates decrease the impacts of climate change through both buffering and decoupling. However, the importance of decoupling depends on the climate change impact assessed. Buffering accounted for 57% and 72% of the change in occupancy probability (for amphipods and calanoid copepods respectively), 90% and 100% of the change in persistence probability, 73% of the change in thermophilization, and 100% of the change in gamma diversity between macro and microclimate predictions (Fig. 2). The effects of decoupling decreased in models that predicted a smaller difference in warming between the coolest and warmest pools (Fig. S5).

Currently, warm and moderate-temperature microclimates can be suitable for one or both cold-adapted organisms, respectively (Fig. 3C). However, microclimate predictions suggest both organisms will be lost in these microclimates in the future, making cool microclimates critical to the persistence of cold-adapted organisms. Cool microclimates will also become suitable for warm-adapted organisms in the future (Fig. 3C), which has important conservation implications. Currently, many of the most biodiverse pools have moderate-temperature microclimates (e.g., green point in Fig. 3A). Consequently, without climate change, conserving the 10 currently most biodiverse pools results in a 100% probability of conserving all 13 organisms. However, the loss of cold-adapted organisms in moderate-temperature microclimates under climate change reduces the value of protecting the 10 currently most biodiverse pools. In the future, the probability of conserving all 13 organisms decreases to 1 - 33% depending on the climate model (Fig. 4). In contrast, cool pools currently lack warm-adapted organisms and therefore protecting the 10

coolest pools results in only a 29% probability of conserving all organisms without climate change (Fig. 4). However, because the coolest pools both preserve cold-adapted organisms and gain warm-adapted organisms under climate change, they often transition from being some of the least to the most biodiverse pools (Fig. 3). Therefore, protecting the 10 coolest pools results in a 97 - 100% probability of conserving all 13 organisms under climate change, depending on the climate model (Fig. 4). Thus, protecting the coolest locations on the landscape becomes an efficient means of conserving current biodiversity under climate change.

Critical Thermal Maximum and Extreme Temperatures:

The average critical thermal maximum ranged between 32.3°C and 38.1°C among the organisms tested (Fig. 5B). Water boatman and calanoid copepods, which our statistical models identified as warm and cold-adapted organisms, had the second highest CTmax (37.3°C) and lowest CTmax values, respectively (Fig. 5B). Macroclimate data predicts that annual maximum temperatures will exceed the critical thermal maximum of cold-adapted organisms in 20 - 36% of the 30 future years, but will never exceed the critical thermal maximum of warm-adapted organisms (Fig. 5A and S6). Microclimate data suggests that annual maximum temperatures in the warmest pools will exceed the critical thermal maximum of cold-adapted organisms in all future years, and warm-adapted organisms in 13 - 63% of future years depending on the climate model (Fig. 5A and S6). However, future annual maximum water temperatures are never predicted to exceed the critical thermal maximum of cold- or warm-adapted organisms in pools with the coolest microclimates (Fig. 5A and S6).

Artificial Pools:

Between June and August 2017, maximum temperatures in both warming treatments were 2.7°C (SE = 0.01°C) warmer than controls (Fig. S8), which is similar to other aquatic

warming studies (Netten et al. 2008). Maximum temperatures reached a high of 32.9°C and 32.4°C in warmed and warmed-plus-precipitation pools, respectively, versus only 28.8°C in control pools. This is similar to the maximum temperatures we predicted for cool microclimates in the future. Unfortunately, water depths decreased precipitously in all treatments between June and August, and water depth in both warmed treatments never recovered from the lack of precipitation during the initial 37 days (Fig. S8). Warmed pools were 34.8% (SE = 1.8%) and warmed-plus-precipitation pools were 29.8% (SE = 1.8%) shallower than control pools on average. The precipitous decline in water depth between June and August also led to a significant increase in conductivity. Conductivity was 126.8% (SE = 13.9%) higher in warmed and 75.1% (SE = 11.9%) higher in warmed-plus-precipitation pools relative to controls in August.

Despite the harsh conditions in both warming treatments, we found 14 taxa in at least one artificial pool, and an average of 6.1 organisms (SE = 0.21) per pool. Average alpha diversity was 6.2 (SE = 0.33) in controls, 6.3 (SE = 0.40) in warmed, and 5.7 (SE = 0.40) in the warmed plus precipitation treatments, and did not differ significantly among treatments (Friedman test: $p = 0.702$). Treatment was significant, but explained only 9.7% of the variation in community structure among pools (Fig. 6). Differences between control and warmed treatments were primarily due to lower *Daphnia magna* occupancy in warmed pools (Table S2). Predacious diving beetles were also more likely to occupy warmed than control pools, but this was not true in the warmed-plus-precipitation treatment (Table S2).

Between June and September 2018, maximum water temperatures in the warming treatments were 2.5°C (SE = 0.01°C) warmer than controls (Fig. S8). Maximum temperatures reached a high of 32.7°C in warmed pools versus only 30.1°C in control pools. Water depths in

warmed pools were 13.9% (SE = 0.6%) shallower than controls on average across the season (Fig. S8) and conductivity was 11.0% (SE = 2.2%) higher in warmed compared to control pools.

Despite only seeding the pools with *D. magna* and ostracods, we detected 11 taxa in at least one of the artificial pools and an average of 6.6 organisms (SE = 0.18) per pool, suggesting many rock pool organisms have a high colonization ability. Alpha diversity was higher in warmed (7.1, SE = 0.27) compared to control pools (6.0, SE = 0.30) although the difference was not significant (Wilcoxon signed-rank: $p = 0.075$). Treatment explained only 15.0% of the variation in community structure among pools but was not significant (PERMANOVA: $p = 0.062$, Fig. 6). Differences among warmed and control pools were due primarily to higher colonization of warmed pools by *Ceriodaphnia dubia* and water boatman (Table S2). *Ceriodaphnia dubia* colonized two and water boatman colonized three warmed pools, whereas neither organism colonized controls.

DISCUSSION

Here we demonstrate that microclimates can differ dramatically over very short distances even in landscapes with no vegetation and little variation in topography (Fig. 1 and S1). In fact, differences in temperature we observed over less than a meter are similar to changes in air temperature that would occur over a 150 km change in latitude or 1350 m change in elevation in our study region. The temperature differences we observed due to variation in water depth and solar exposure among pools are greater than many of the temperature differences observed due to factors more typically included in microclimate studies (reviewed by Dobrowski 2011, Lenoir et al. 2017). Moreover, we predict that cool locations will warm less than warmer locations (i.e., higher decoupling in cool microclimates; Fig. 1), which will increase the microclimate variation in the future.

Microclimate variation, which is often overlooked in climate change biology, significantly altered predictions of how biodiversity will respond to climate change. Predictions using macroclimate data for our study site are consistent with typical fingerprints of climate change: low occupancy and persistence probabilities results in the predicted loss of cold-adapted organisms, and therefore a decrease in gamma diversity (Fig. 2). These changes are also consistent with patterns of thermophilization observed in many communities affected by climate change (De Frenne et al. 2013, Duque et al. 2015). However, predictions incorporating microclimates suggest cold-adapted organisms could persist in cool microclimates, therefore all 13 organisms are likely to persist in the study area in the future and thermophilization is much reduced (Fig. 2).

Our lab and field experiments also corroborated our statistical predictions in a few key ways. First, of the five organisms identified as either cold- or warm-adapted by our statistical model, two of three evaluated (calanoid copepod and water boatman) had a critical thermal maximum consistent with their identity as cold- and warm-adapted. Second, comparing predicted maximum temperatures to CT_{max} of cold-adapted organisms confirms that macroclimate data overestimates the threat to cold-adapted organisms by ignoring cool microclimates that could provide refuge. Third, warmer microclimates will become unsuitable for cold-adapted organisms, at least during warm parts of some years. Also, in extreme years, maximum temperatures could exceed the critical thermal maximum of warm-adapted organisms, which further stresses the importance of moderate-temperature and cool microclimates, even for the persistence of warm-adapted organisms. Fourth, many organisms naturally colonized the artificial pools, including organisms that we predict to colonize newly suitable habitat in the future (e.g., water boatman). Moreover, water boatman only colonized warmed pools in 2018

further corroborating our predictions that water boatman both prefer warmer pools and might contribute to increases in alpha diversity in the future. Fifth, we found both warm and cold-adapted organisms in warmed pools, suggesting that these organisms will be able to coexist in a warmer environment. Last, factors that we did not account for in our model, such as extreme increases in conductivity, had little impact on biodiversity. Indeed, we originally included conductivity as a covariate in our MSOM, but removed it because no organism was predicted to be sensitive to conductivity.

A growing number of studies are demonstrating that microclimates can reduce the observed (Maclean et al. 2015) and predicted impacts of climate change (reviewed in Lenoir et al. 2017, Lembrechts et al. 2019). For example, Randin (2009) demonstrated that up to 100% of plant species predicted to go locally extinct in the Swiss Alps using macroclimate data are predicted to persist when microclimates are accounted for. In fact, all studies that compared predictions of species persistence under climate change using microclimate (< 30 m resolution) and macroclimate (> 1 km resolution) data have shown increased persistence in models accounting for microclimates (Lenoir et al. 2017). Community-level impacts of climate change, such as thermophilization, are also reduced in cool microclimates (De Frenne et al. 2013, Duque et al. 2015). However, most studies evaluating the buffering effect of microclimates in climate change biology focus on topographically diverse or forested landscapes where large microclimate variation is expected. Our results extend these conclusions by suggesting that even areas with little topographic variation or vegetation could experience buffering effects due to microclimates. Significant microclimate variation has been observed in many other seemingly homogenous landscapes including peat bogs (van der Molen and Wijnstra 1994, Turlure et al. 2010), talus fields (Varner and Dearing 2014), and grasslands (Thomas et al. 2009). Hence,

microclimate buffering might be much more widespread than previously assumed, although still likely highest in topographically diverse and forested landscapes (Luoto and Heikkinen 2008, Suggitt et al. 2018).

The buffering effect of microclimates is a critical aspect of climate to consider for biodiversity conservation under climate change. Although evidence suggests that climate change impacts are reduced in cool microclimates (Maclean et al. 2015) and topographically diverse landscapes (Luoto and Heikkinen 2008, Suggitt et al. 2018), the value of protecting microclimates relative to other conservation strategies has not been evaluated previously. Our results clearly demonstrate the value of protecting cool microclimates for the preservation of cold-adapted organisms in the study area. However, because we also predict cool microclimates will become suitable for warm-adapted organisms under climate change, protecting just a small number of cool microclimates also becomes an efficient means of conserving all focal organisms that currently occur in our study area. Furthermore, protecting cool microclimates is a significantly better strategy than conserving current biodiversity hot spots, which is a commonly utilized strategy worldwide (Myers et al. 2000). Our results therefore support recommendations to conserve landscapes with high microclimate variation. Our results also highlight the importance of cool microclimates in particular, which could be an important tool for conserving species that currently occur in a protected area. Existing protected areas might even consider management actions to increase the number of cool microclimates. Creating cool microclimates has rarely been recommended in the climate change adaptation literature, but could be a very cost-effective means of conserving species that occur in protected areas (Greenwood et al. 2016).

Microclimates can reduce the impacts of climate change by remaining suitable for focal species despite experiencing the same amount of climate change as other locations (i.e.,

buffering) or because microclimates are less affected by climate change relative to surrounding areas (i.e., decoupling). Cool pools in our study area will likely provide both benefits to cold-adapted organisms in the future, as they remain suitable for cold-adapted organisms despite warming, but also warm less than warmer pools. Other studies have also demonstrated that cool locations provide both buffering and decoupling benefits (Pepin et al. 2011, Gollan et al. 2014, McCullough et al. 2016, Lenoir et al. 2017, Maclean et al. 2017). For example, Maclean et al. (2017) demonstrated that warming between 1979-2014 ranged between 0.87°C and 1.16°C among locations on the Lizard Peninsula in the United Kingdom, but the lowest rates of warming were on cool northeast facing slopes. However, not all cool locations are decoupled from climate change and some cool locations might warm more than warmer locations (Gillingham et al. 2012, Gollan et al. 2014). Consequently, understanding the relative value of buffering and decoupling has important implications for identifying the proper type of microclimates to protect as a conservation strategy (Gollan et al. 2014). Here, we show that much of the effect of microclimates was due to buffering, although decoupling had large effects on the occupancy probability of the most threatened organism, amphipods. These results are similar to the only other study we are aware of to evaluate the relative value of buffering and decoupling. Lenoir et al. (2017) also demonstrated that decoupling increased the occupancy probability of a simulated species, but only 15% of the difference between predictions using macroclimate and microclimate data were due to decoupling. Protecting microclimates that provide both buffering and decoupling effects is likely the best conservation strategy, although these sites might be rare (Gollan et al. 2014). More research is needed to better understand the relative value of buffering and decoupling to help design effective and efficient climate change adaptation strategies.

Like many attempts to predict future species distributions, our results have some important caveats. Our statistical predictions of future water temperature should be interpreted with caution because we are predicting into future conditions not currently observed at our study site (Lenoir et al. 2017, Lembrechts et al. 2019). However, our water-temperature model does take some important future changes into account including changes in water depth and the non-linear relationship between air temperature and water temperature due to evaporative cooling (Mohseni et al. 1998, Morrill et al. 2005, Harvey et al. 2011). There are also important biological uncertainties. We trained the MSOM with data from a very small portion of the range of each focal organism, which could affect the occupancy-habitat relationships we identified. However, results from our CTmax and artificial-pool experiments help validate our results. Also, if species are locally adapted, local models might perform better than models trained from data throughout a species range (Hällfors et al. 2016, Peterson et al. 2019). We also only model the future probability of occupancy in each pool. We do not consider meta-community dynamics. Our artificial warming experiments provide some evidence that species can coexist and that species will be able to colonize newly suitable locations. However, a key remaining question in most microclimate and climate change refugia studies is the number and spatial configuration of patches needed to maintain a sustainable and genetically diverse meta-population of focal species. Incorporating metacommunity dynamics, including stochastic extirpations, dispersal, genetic diversity, and species interactions is an important next step in climate change biology.

We also do not incorporate the potential for novel species to colonize our study site in the future. Species with a higher temperature tolerance than any species currently in the community are likely to colonize warmer rock pools in the future. New species could increase gamma diversity, increase alpha diversity in warmer microclimates, and increase thermophilization.

However, our primary conclusions would remain the same: cold-adapted organisms that currently occur at our study site could persist in cool microclimates, which would maintain higher gamma diversity and reduce thermophilization, relative to macroclimate predictions. Moreover, if conserving species that currently occur in an area is the conservation goal, our results suggest protecting cooler microclimates is the best conservation strategy. If conserving biodiversity *per se* or facilitating change is a conservation goal (Anderson and Ferree 2010, Urban 2020), then protecting just the coolest locations on the landscape could be counterproductive. Warmer microclimates could remain the most biodiverse locations on the landscape if novel species colonize the study site in the future. Therefore, warmer microclimates could be important for conserving the largest number of species. Moreover, warmer microclimates could act as important stepping stones for range-shifting species (Hannah et al. 2014). Losing warmer microclimates could thus increase the vulnerability of species at a regional scale. Ideally, conservation strategies will balance the competing objectives of local and regional biodiversity conservation, such as conserving a range of microclimates. It will also be critical to evaluate whether novel species interactions will impact local biodiversity (Wallingford et al. 2020).

The fingerprints of climate change are clear, but inconsistent around globe and among species. Explaining this variation is an important next step in climate change biology. A number of hypotheses have been proposed to explain variation in climate change responses, but few have strong support on their own. For example, species traits (e.g., body size, dispersal ability) explain only a small amount of variation in observed range shifts and phenological responses among species, especially outside marine environments (Angert et al. 2011, Buckley and Kingsolver 2012, Sunday et al. 2015, MacLean and Beissinger 2017). Changes in climate variables other

than temperature might also explain unexpected species responses (Crimmins et al. 2011, Tingley et al. 2012, VanDerWal et al. 2013). The buffering effects of microclimates are emerging as another compelling hypothesis that regularly explains variation in climate change impacts, and likely interacts with the other hypotheses. Moreover, the buffering effect of microclimates offers a potentially cost-efficient means of conserving species under climate change. Hence, it is critical to move beyond macroclimate explanations for observed climate change responses, and start to incorporate microclimates into predictions in climate change biology if we hope to gain an accurate picture of climate change impacts worldwide. Determining the optimal spatial resolution to balance the computational costs of microclimate analyses and the biological realism necessary to make accurate future predictions is a necessary next step (Potter et al. 2013, Bennie et al. 2014, Nadeau et al. 2017b).

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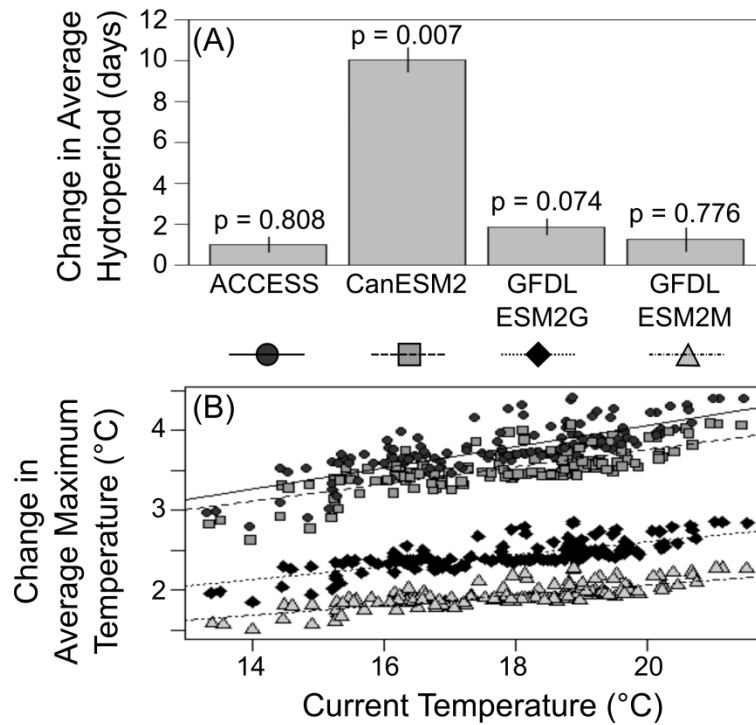


Figure 1. The effects of climate change on the hydroperiod and temperature in 149 freshwater rock pools based on four different climate models (see methods). (A) The mean change (± 1 SE) in the average hydroperiod between the current (1989 - 2018) and future period (2071 - 2100). The p-values above each bar are from paired Wilcoxon signed rank tests evaluating whether the average hydroperiod differed among the current and future period. (B) The change in average maximum temperature in each pool between the current and future period versus the current average maximum temperature in the pool. Symbols and line types correspond to different climate models as shown above the panel. The slope of the relationship between change in temperature and current temperature for each climate model is: ACCESS, 0.13 (SE = 0.009); CanESM, 0.11 (SE = 0.008); GFDL-ESM2G, 0.08 (SE = 0.006); and GFDL-ESM2M, 0.06 (SE = 0.004). All slopes are significantly different from zero ($p < 0.001$).

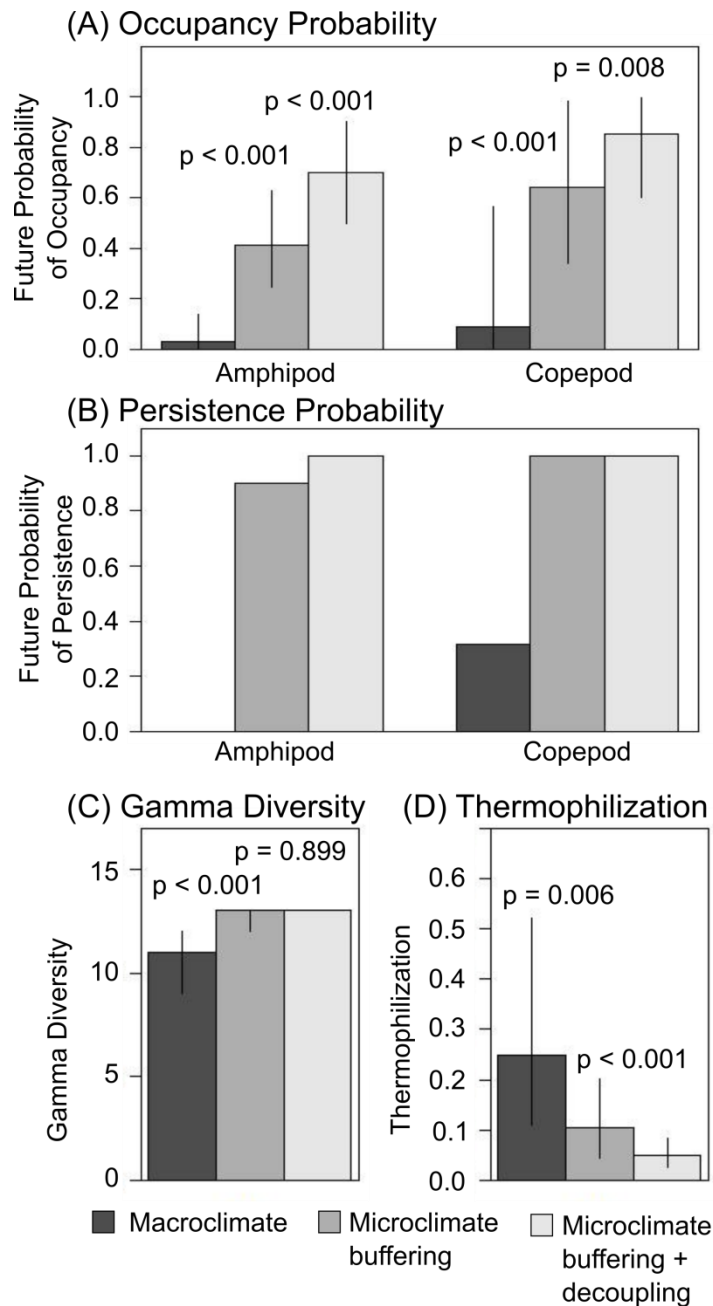


Figure 2. Differences in site-level impacts of climate change on biodiversity as predicted from macroclimate data (left bar), microclimate data including buffering (i.e., all locations warm equally; middle bar), microclimate data including buffering and decoupling (i.e., differential warming among locations; right bar). We include predictions of the following climate change impacts from a multi-species occupancy model that identified occupancy-habitat relationships for 13 organisms: (A) estimates of occupancy probability for two cold-adapted organisms, (B) estimates of persistence probability based on estimated presence/absence data for two cold-adapted organisms, (C) estimates of gamma diversity, and (D) estimates of thermophilization (see methods). Bars are medians and error bars are 95% credible intervals. P-values are the proportion of posterior predictions that predicted no difference or a difference opposite of that predicted between the macroclimate predictions and microclimate buffering predictions (left), and the microclimate buffering predictions and microclimate buffer + decoupling predictions (right).

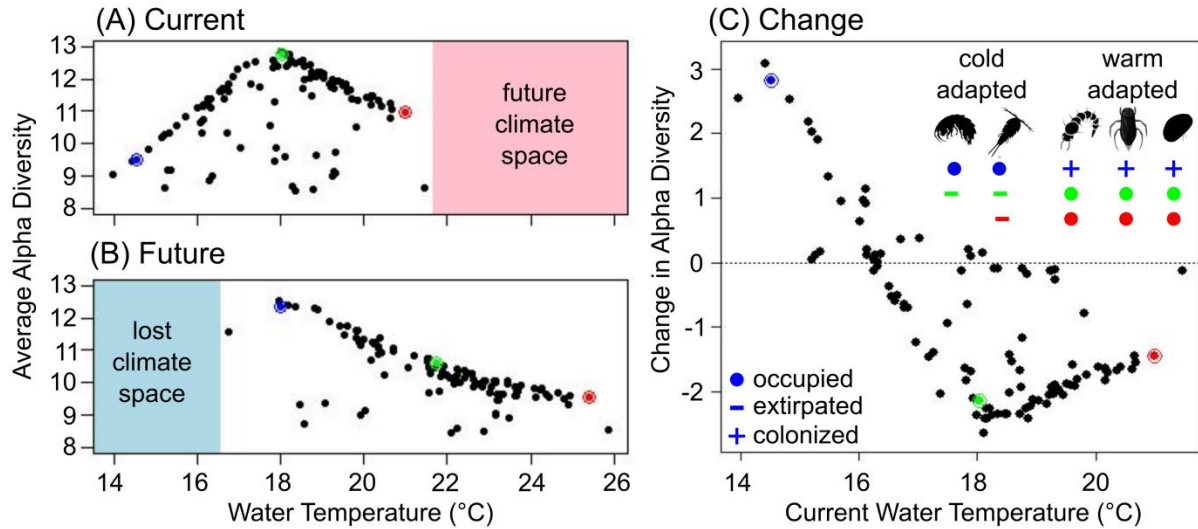


Figure 3. Average alpha diversity in 107 freshwater rock pools with different microclimates as predicted by a multi-species occupancy model in (A) the current period (1981 - 2018) and (B) a future period (2071 - 2100) using the ACCESS climate model. (C) The change in average alpha diversity between the current and future period. Results from the other three climate models are shown in Fig. S6. Three pools are highlighted to demonstrate how average alpha diversity is predicted to change in cool (blue point), moderate-temperature (green point), and warm microclimates (red point). Predicted changes in community composition are shown in the upper right of panel C. Organisms include (from left to right): amphipod, calanoid copepod, mosquito larvae, water boatman, and ostracod. Circles represent presence in both periods, + signs represent gain of the organism in the future, - signs represent loss of the organism in the future, and no symbol represents absence of the organism in both periods. The color of the symbols matches the highlighted pools in all three panels.

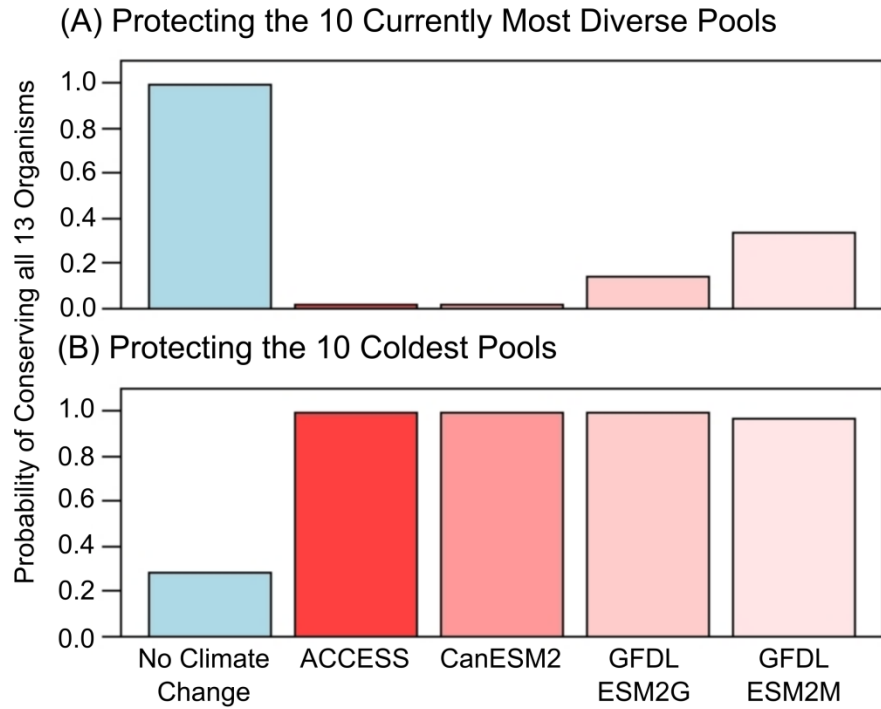


Figure 4. The probability of conserving all 13 organisms in our study area using two different conservation strategies: (A) conserving the 10 currently most biodiverse pools, and (B) conserving the 10 coolest pools. The blue bars are predictions assuming no climate change. The red bars are outputs from different climate models that predict different amounts of climate change (see Methods).

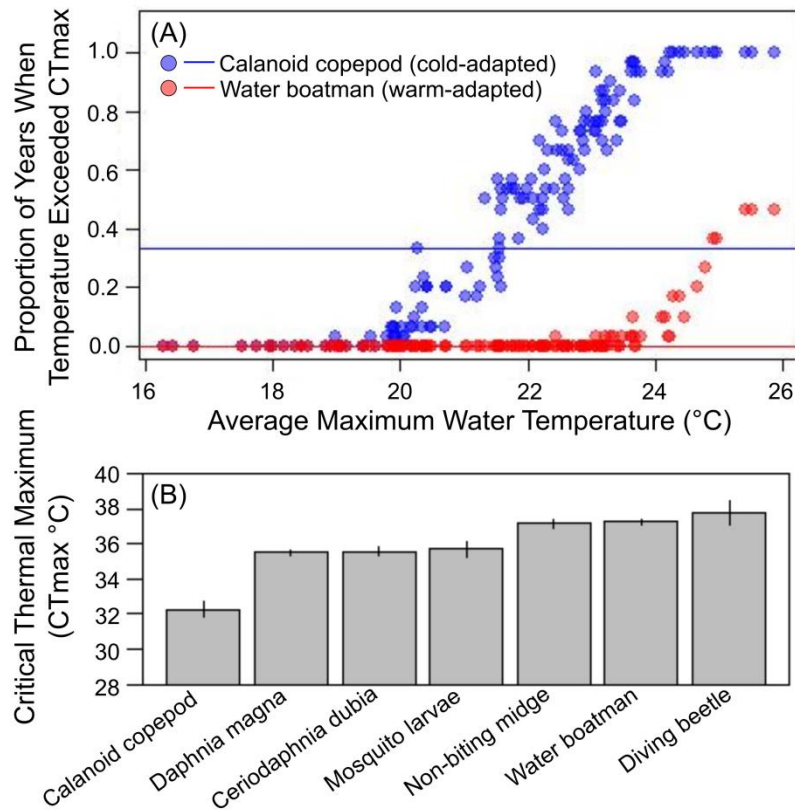


Figure 5. (A) The proportion of future years (2071 - 2100) under the ACCESS climate model when annual maximum water temperatures are predicted to exceed the critical thermal maximum (CTmax) of a cold-adapted organism (calanoid copepod; blue) and a warm-adapted organism (water boatman; red) in 107 freshwater rock pools with different microclimates. Each point represents a pool. Horizontal lines represent macroclimate predictions (i.e., the proportion of future years when the average annual maximum temperature among pools is expected to exceed the critical thermal maximum of each organism). (B) Average critical thermal maximum (\pm SE) of seven organisms (see Table S1 for taxonomic classification).

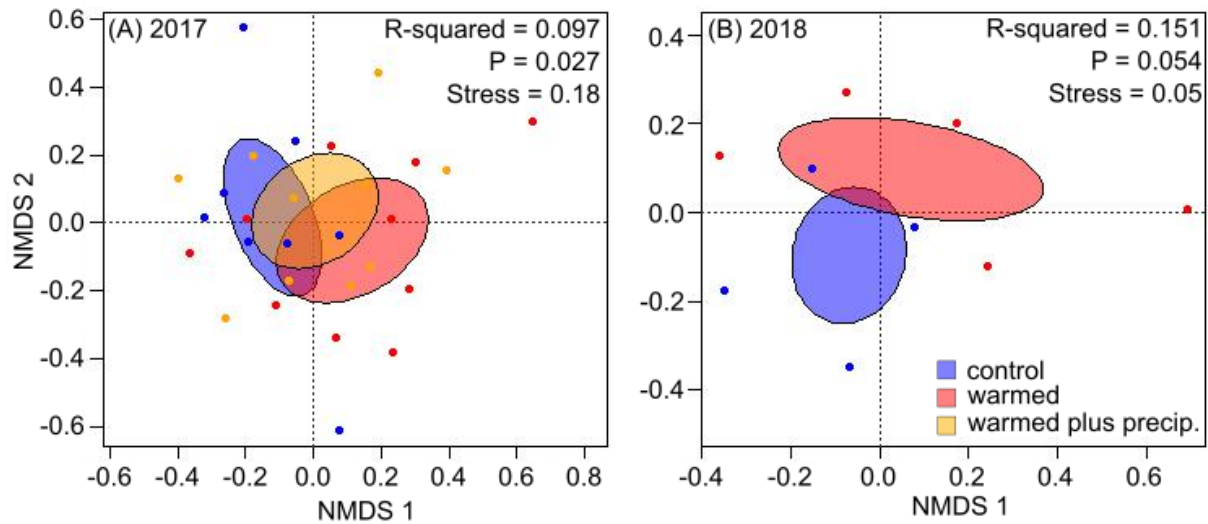


Figure 6. Non-metric multidimensional scaling (NMDS) ordinations of community composition in the three artificial pool treatments in (A) 2017 and (B) 2018. Points show the location of each pool and ellipses show the 95% confidence interval of the centroid for each treatment. R-squared and p-values in the upper right are from PERMANOVA analysis. Stress is a measure of the degree to which this two-dimensional representation summarizes the observed distances among communities. Stress values less than 0.2 are typically considered good.

SUPPLEMENTAL MATERIALS

Supplemental Tables:

Table S1: A list of focal organisms included in the multi-species occupancy models. Asterisks denote the taxonomic resolution of identification in the field. Organisms without asterisks were only observed using a microscope in the lab. Despite not always being able to identify organisms to highest taxonomic level in the field, rarely did detailed identification under a microscope lead to a different identification than the highest resolution presented. For example, *D. magna* and mosquito larvae could only be identified to genus and family (respectively) in the field.

However, only one sample out of hundreds identified under the microscope resulted in an identification other than *D. magna* or *Aedes sp.* Hence, for samples we did not process under a microscope, we assumed all organisms were at the highest taxonomic level provided in the table. This assumption could result in uncertainty in occupancy-habitat relationships, but is unlikely to affect our overall conclusions.

Common Name	Class	Order	Family	Genus	Species
Ostracod	Ostracoda	Podocopida*			
Water boatman	Insecta	Hemiptera	Corixidae*	Trichocorixa	verticalis
Predacious diving beetle	Insecta	Coleoptera	Dytiscidae*	Neoporus	
Aquatic springtail	Entognatha	Poduromorpha	Poduridae	Podura	aquatica
Water mite	Arachnida	Trombidiformes	Hydrachnidae		
Amphipod	Malacostraca	Amphipoda*			
Daphnia magna	Branchiopoda	Cladocera	Daphniidae	Daphnia*	magna
Ceriodaphnia dubia	Branchiopoda	Cladocera	Daphniidae	Ceriodaphnia*	dubia
Non-biting midges	Insecta	Diptera	Chironomidae*		
Chydorus sphaericus	Branchiopoda	Cladocera	Chydoridae*	Chydorus	sphaericus
Mosquito larvae	Insecta	Diptera	Culicidae*	Aedes	
Calanoid copepod	Copepoda	Calanoida			
Cyclopoid copepod	Copepoda	Cyclopoida			

Table S2: Contributions of each organism to the dissimilarity among artificial pool treatments in 2017 and 2018. C = control, W = warmed, and W+P = warmed plus precipitation. Cont. is the average contribution of the organism to the between-group dissimilarity. P-values are from permutation tests. Organisms that contributed significantly to the between group dissimilarities are highlighted in bold. See table S1 for the taxonomic classification of each organism.

Organism	2017							2018			
	Number of Pools			Control versus Warmed		Control versus Warmed + Precip.		Number of Pools		Control versus Warmed	
	C	W	W+P	Cont.	p-value	Cont.	p-value	C	W	Contribution	p-value
Amphipod	0	2	1	0.01	0.506	0.01	0.811	0	0	0.00	1.000
C. dubia	6	5	5	0.04	0.879	0.04	0.324	0	2	0.02	0.033
Calanoid copepod	1	0	0	0.01	0.462	0.01	0.061	0	1	0.01	0.011
Non-biting midge	10	9	10	0.01	0.447	0.00	1.000	8	7	0.01	0.011
C. sphaericus	9	10	8	0.01	0.89	0.02	0.122	8	8	0.00	1.000
Water boatman	3	3	1	0.03	0.266	0.03	0.696	0	3	0.03	0.016
Mosquito larvae	2	1	3	0.02	0.908	0.03	0.260	5	8	0.03	0.135
Cyclopoid copepod	10	10	10	0.00	1	0.00	1.000	8	8	0.00	1.000
D. magna	6	2	3	0.05	0.012	0.05	0.018	8	8	0.00	1.000
Diving beetle	0	3	0	0.02	0.038	0.00	1.000	0	0	0.00	1.000
Harpacticoid copepod	0	3	1	0.03	0.174	0.01	0.993	0	0	0.00	1.000
Ostracoda	5	4	4	0.04	0.671	0.04	0.107	8	8	0.00	1.000
Aquatic springtail	2	2	1	0.02	0.45	0.02	0.544	0	1	0.01	0.030
Water mite	8	9	10	0.02	0.287	0.02	0.369	3	3	0.03	1.000

Supplemental Figures:

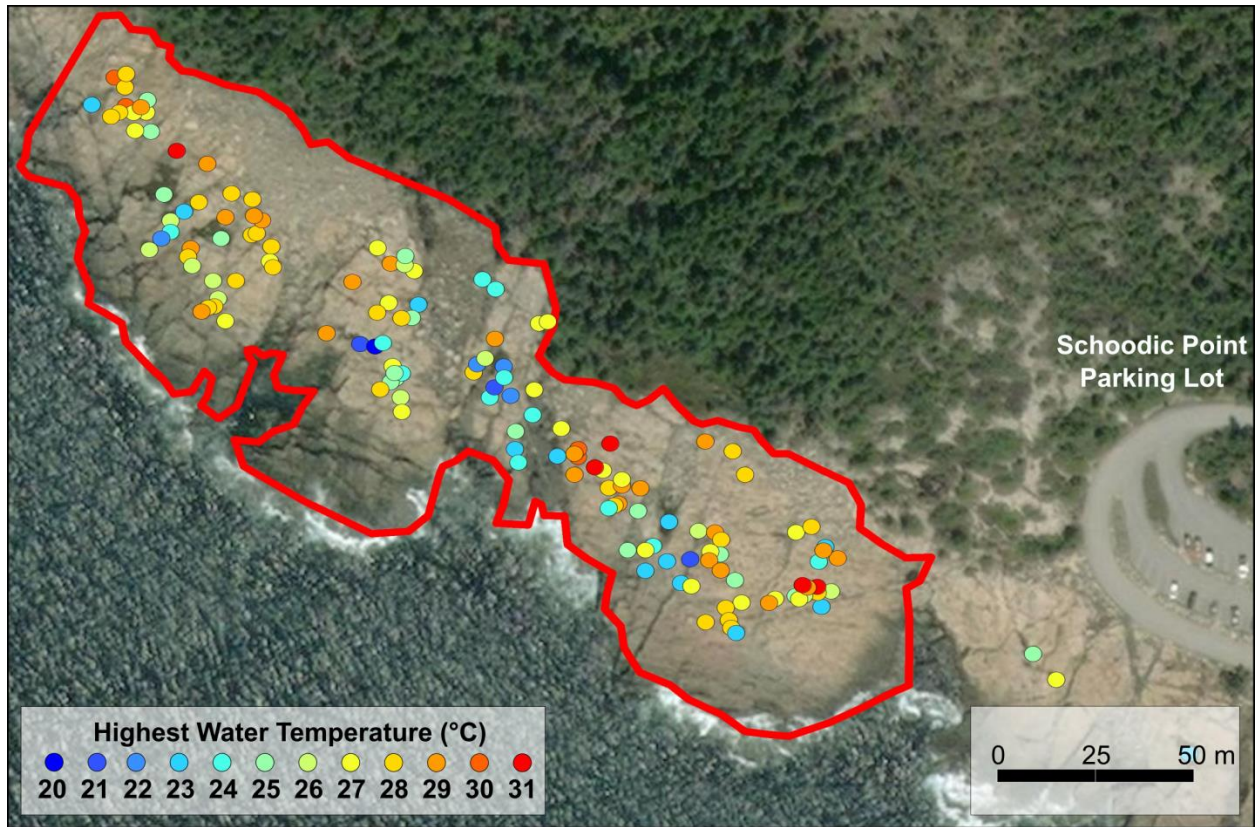


Figure S1. Study area (bold red line) located on Schoodic Point in Acadia National Park, Maine, United States. We mapped 149 freshwater rock pools (colored circles) in the study area. Circle color represents the average annual highest temperature in the period 1989 - 2018 based on statistical models (see methods).

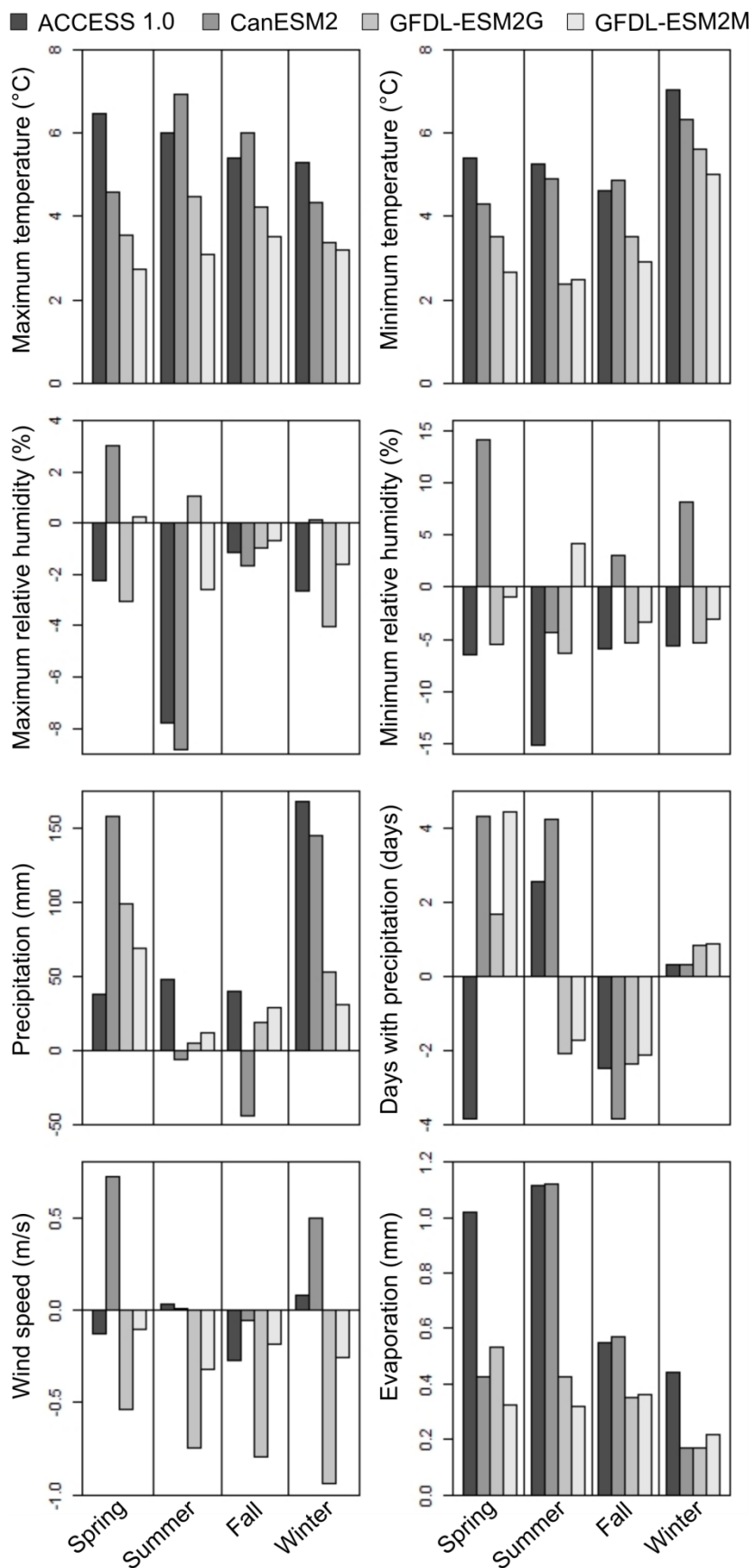


Figure S2. Climate change projections from four climate models for eight variables. In all cases, bars represent differences between model projections from the historical period (1989 - 2018) and the future period (2071 - 2100). We calculated evaporation using the Penman Equations (see methods). The earth systems models included: (1) The Australian Community Climate and Earth System Simulator coupled model (ACCESS 1.0); (2) The Canadian Earth System Model (CanESM2), and two variants of the Geophysical Fluid Dynamics Laboratory's Earth Systems Model (GFDL) (3) ESM2G and (4) ESM2M.

(A) 2017



(B) 2018



Figure S3. Artificial freshwater rock pools used to evaluate the effects of warming at the whole-ecosystem scale in (A) 2017 and (B) 2018. In 2017, we included three treatments: (1) control, (2) warming, and (3) warming plus precipitation. In 2018, we included two treatments: (1) control and (2) warming. We fit both warming treatments with an open-top greenhouse and the control with a mesh top. In 2018, we redesigned the greenhouse and mesh tops to funnel precipitation into the pool.

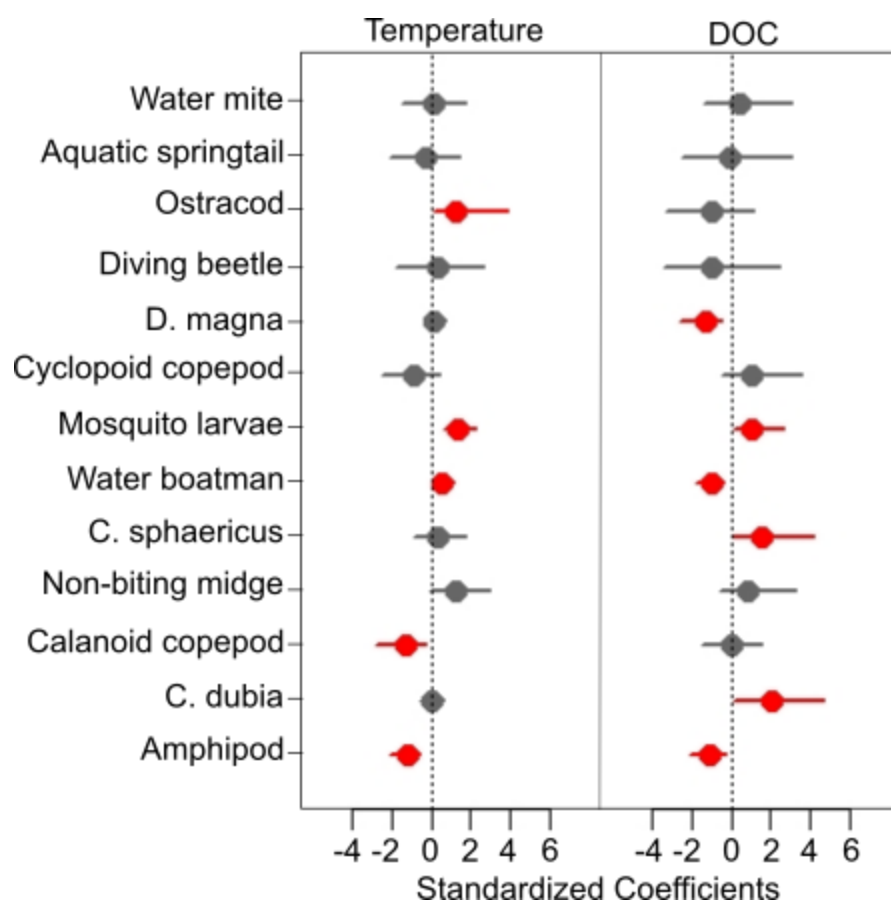


Figure S4. Standardized coefficients from the final multi-species occupancy model used to predict current and future occupancy of freshwater rock pool organisms. DOC is dissolved organic carbon. Red points and lines highlight coefficients where the 95% CI does not overlap zero. See Table S1 for taxonomic classification of each organism.

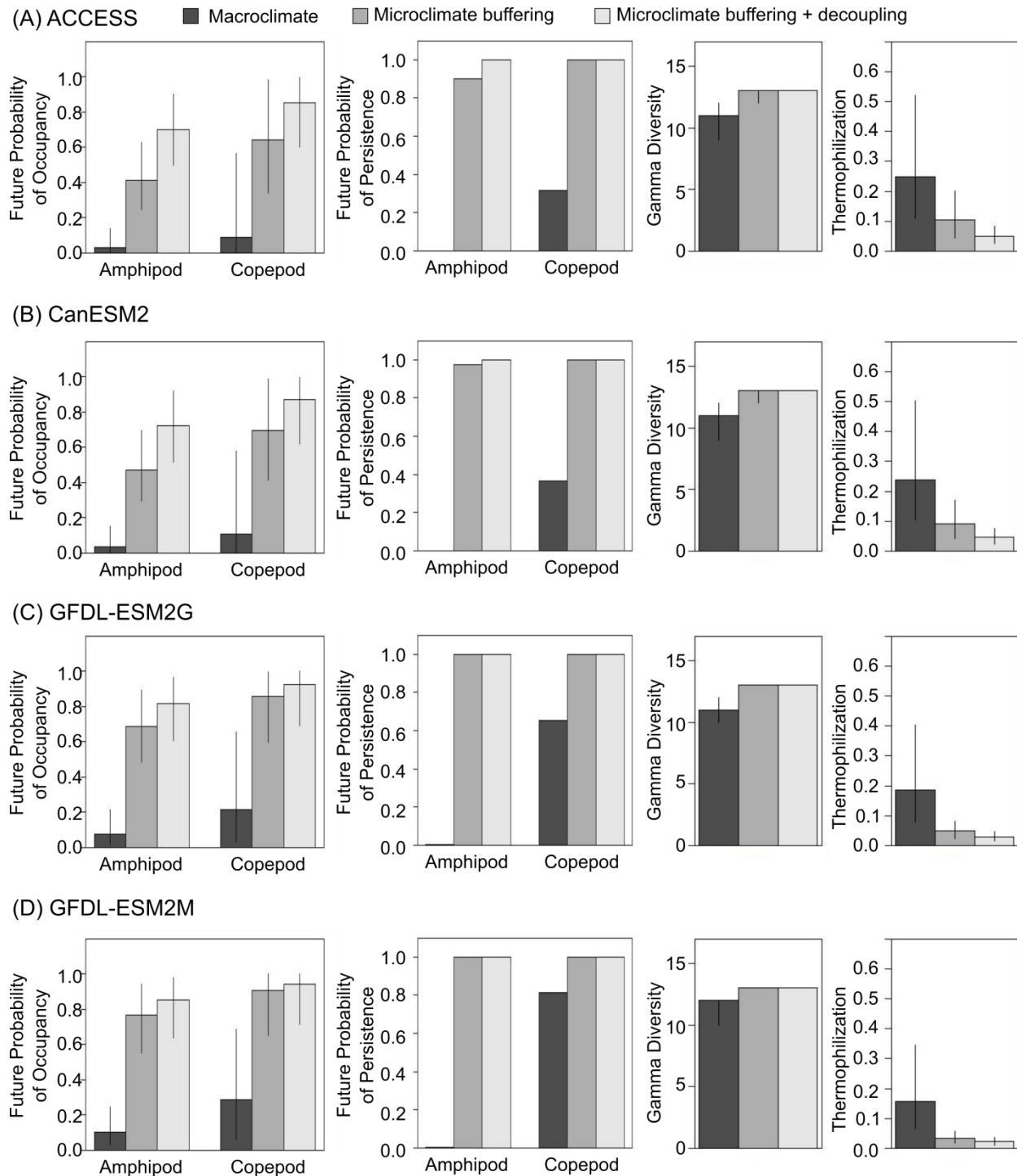
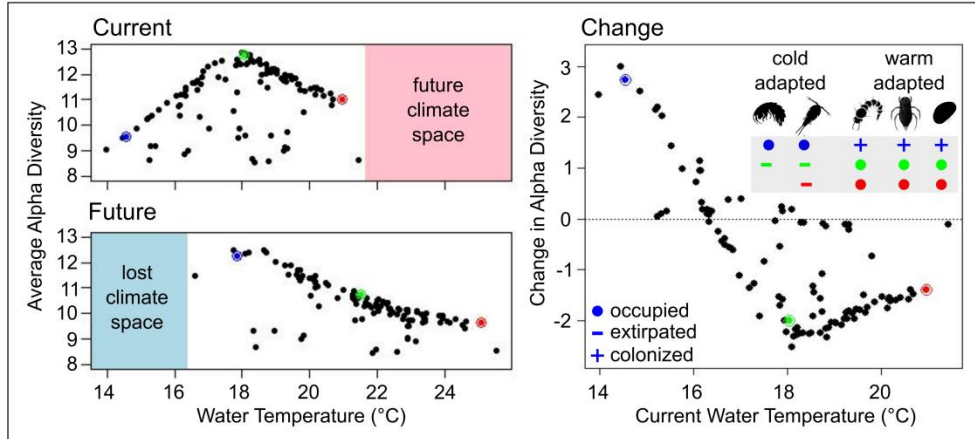
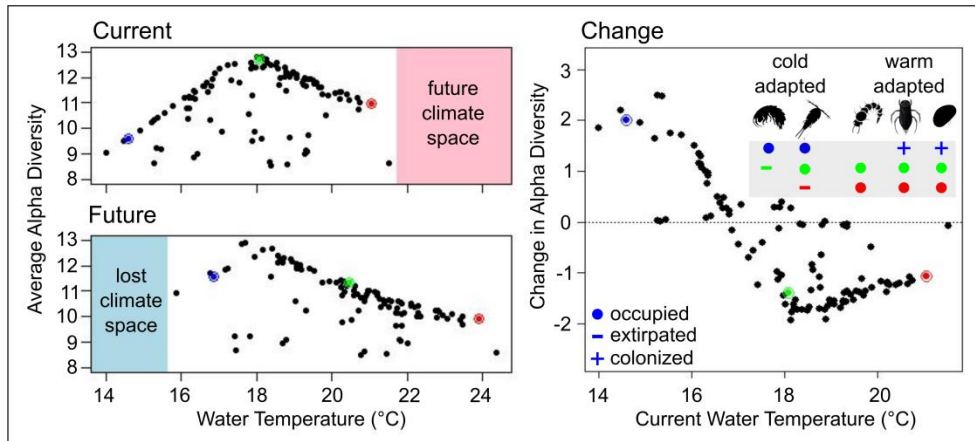


Figure S5. Differences in site-level impacts of climate change predicted from macroclimate data (left bar), microclimate data including buffering (i.e., all locations warm equally; middle bar), microclimate data including buffering and decoupling (i.e., differential warming among locations; right bar) from four different climate models. See methods and Fig. 2 for more information.

CanESM2



GFDL-ESM2G



GFDL-ESM2M

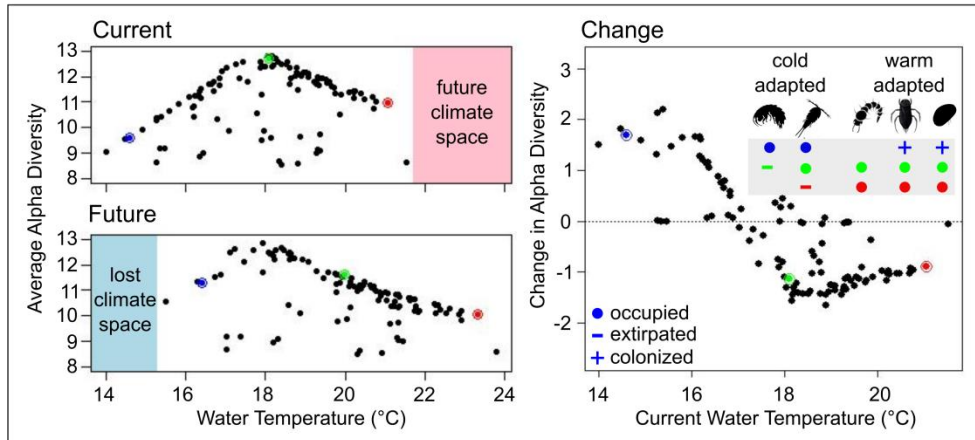


Figure S6: Average alpha diversity in 107 freshwater rock pools with different microclimates as predicted by a multi-species occupancy model in the current period (1981 - 2018), and a future period (2071 - 2100), and the change in average alpha diversity between the current and future period. Results are presented for three different climate models (see methods): CanESM2 (top), GFDL-ESM2G (middle), and GFDL-ESM2M (bottom). See Fig. 3 for more details.

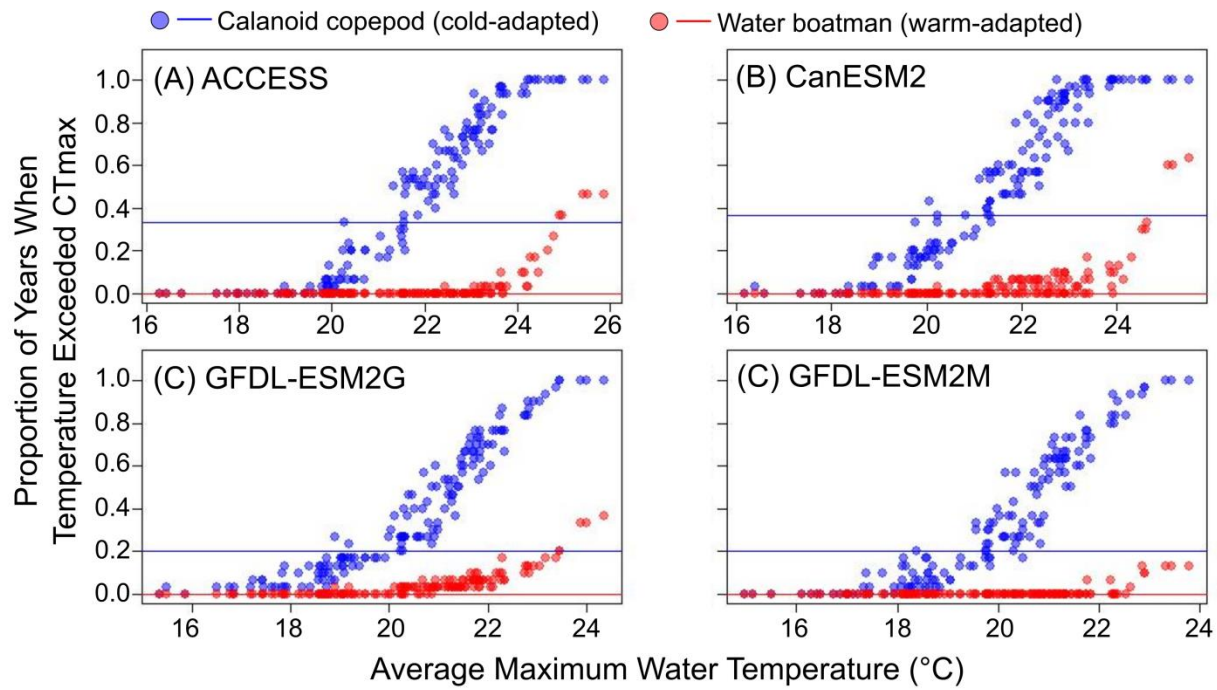


Figure S7. The proportion of future years (2071 - 2100) under four different climate models (see methods) when annual maximum water temperatures are predicted to exceed the critical thermal maximum (CTmax) of a cold-adapted organism (Calanoid copepod; blue) and a warm-adapted organism (Water boatman; red) in 107 freshwater rock pools with different microclimates. Each point represents a pool. Horizontal lines represent macroclimate predictions (i.e., the proportion of future years when the average annual maximum temperature among pools is expected to exceed the CTmax of each organism).

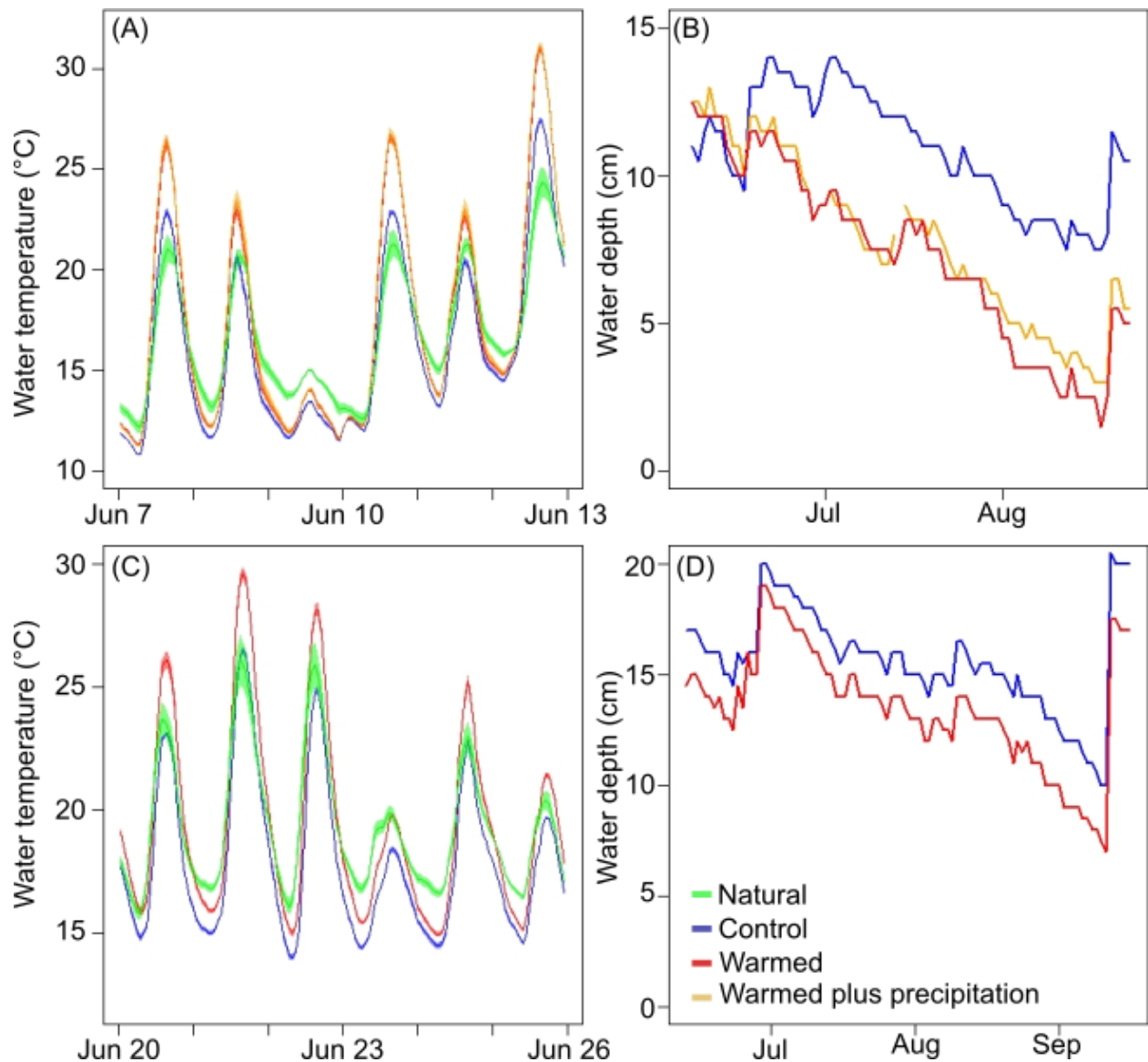


Figure S8. Average water temperature (A, C) and water depth (B, D) in three artificial rock pool treatments and paired natural pools in 2017 (top) and 2018 (bottom). Temperature data is shown for one week at the beginning of the experiment when water depths within the treatments were comparable. Water depths are shown for the duration of the experiment. Shaded areas in A and C are ± 1 SE from the different pools in each treatment.

Non-threshold Approach to Predict Presence/Absence:

We simulated posterior predictions of presence/absence using a Bernoulli distribution with a probability equal to the estimated occupancy probability for each organism in each pool. This is equivalent to the way an MSOM estimates the latent true occupancy state z , except here we apply the approach to posterior predictions. Generating presence/absence data in this way alleviates the need to use an arbitrary threshold of occupancy probability to estimate if a site is occupied. We converted all the posterior predictions of occupancy probability to presence/absence data using this approach. We used the site with the maximum occupancy probability for each organism to make the microclimate predictions. We then re-evaluated macroclimate and microclimate predictions of gamma diversity (Fig. S9). We did not re-evaluate the probability of persistence because under this approach, and with a large posterior sample, the probability of persistence is equal to the occupancy probability at a site. The other metrics assessed when comparing macro and microclimate predictions do not depend on estimates of presence/absence. We also re-evaluated the pool-level analyses, including changes in alpha diversity among the different microclimates (Fig. S10), and a comparison of the two conservation strategies (Fig. S11). Using this non-threshold approach to generate presence absence data did alter our conclusions (Fig. S9 – S11). However, this approach adds extra stochasticity to the presence/absence predictions, which reduced the effect of decoupling on estimates of future gamma diversity (Fig. S9).

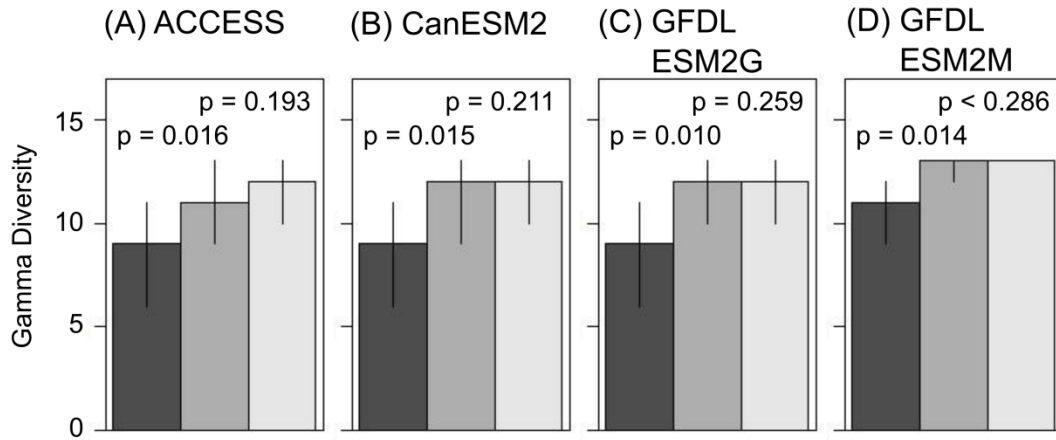


Figure S9. Differences in future gamma diversity as predicted from models using macroclimate data (left bar), microclimate data including buffering (i.e., all locations warm equally; middle bar), microclimate data including buffering and decoupling (i.e., differential warming among locations; right bar) from four different climate models (see methods). Here, we estimated gamma diversity using a non-threshold approach to convert posterior predictions of occupancy probability to presence/absence data. Bars are medians and error bars are 95% credible intervals. P-values are the proportion of posterior predictions that predicted no difference or a difference opposite of that predicted between the macroclimate predictions and microclimate buffering predictions (left), and the microclimate buffering predictions and microclimate buffer + decoupling predictions (right).

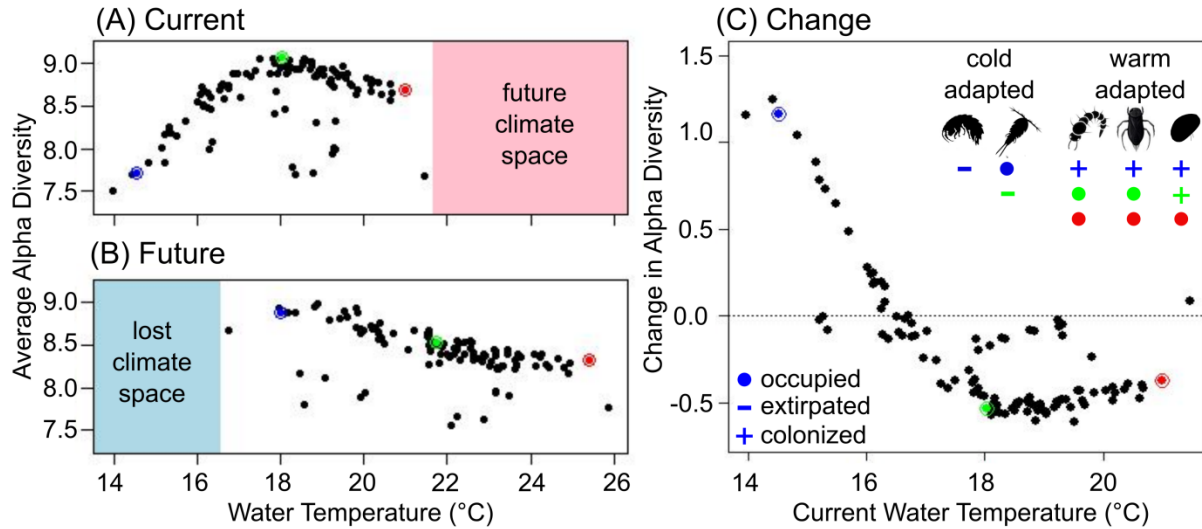


Figure S10. Average alpha diversity in 107 freshwater rock pools with different microclimates as predicted by a multi-species occupancy model in (A) the current period (1981 - 2018) and (B) a future period (2071 - 2100) using the ACCESS climate model. (C) The change in average alpha diversity between the current and future period. Here, we estimated alpha diversity in each pool using a non-threshold approach to convert posterior predictions of occupancy probability to presence/absence data. Three pools are highlighted to demonstrate how average alpha diversity is predicted to change in cool (blue point), moderate-temperature (green point), and warm microclimates (red point). Predicted changes in species composition are shown in the upper right of panel C. The organisms shown are (from left to right): amphipod, calanoid copepod, mosquito larvae, water boatman, and ostracod (see Table S1 for taxonomic classification). No symbol represents absence in both periods, circles represent presence in both periods, + signs represent gain of the organism in the future, and – signs represent loss of the organism in the future. The color of the symbols matches the highlighted pools in all three panels.

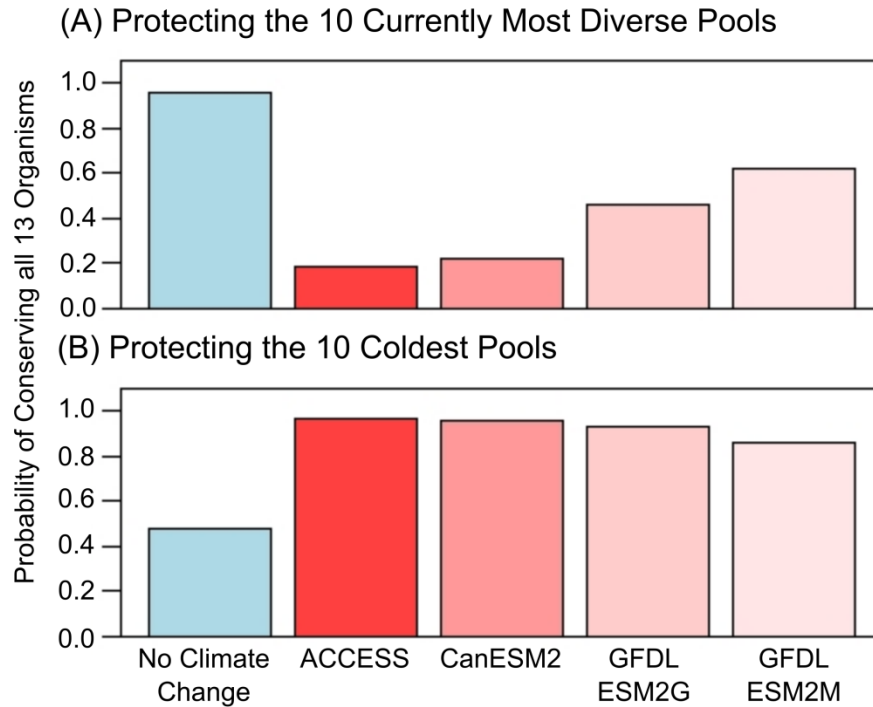


Figure S11. The probability of conserving all 13 organisms in our study area using two different conservation strategies: (A) conserving the 10 currently most biodiverse pools, and (B) conserving the 10 coolest pools. Here, we estimated the presence of each organism in the 10 focal pools using a non-threshold approach to convert posterior predictions of occupancy probability to presence/absence data. The blue bars are predictions from a 30-year current period assuming no climate change. The red bars are outputs from different climate models that predict different amounts of climate change (see Methods).

Chapter 5: Eco-evolution on the Edge During Climate Change

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Review and synthesis

Eco-evolution on the edge during climate change

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We urgently need to predict species responses to climate change to minimize future biodiversity loss and ensure we do not waste limited resources on ineffective conservation strategies. Currently, most predictions of species responses to climate change ignore the potential for evolution. However, evolution can alter species ecological responses, and different aspects of evolution and ecology can interact to produce complex eco-evolutionary dynamics under climate change. Here we review how evolution could alter ecological responses to climate change on species warm and cool range margins, where evolution could be especially important. We discuss different aspects of evolution in isolation, and then synthesize results to consider how multiple evolutionary processes might interact and affect conservation strategies. On species cool range margins, the evolution of dispersal could increase range expansion rates and allow species to adapt to novel conditions in their new range. However, low genetic variation and genetic drift in small range-front populations could also slow or halt range expansions. Together, these eco-evolutionary effects could cause a three-step, stop-and-go expansion pattern for many species. On warm range margins, isolation among populations could maintain high genetic variation that facilitates evolution to novel climates and allows species to persist longer than expected without evolution. This 'evolutionary extinction debt' could then prevent other species from shifting their ranges. However, as climate change increases isolation among populations, increasing dispersal mortality could select for decreased dispersal and cause rapid range contractions. Some of these eco-evolutionary dynamics could explain why many species are not responding to climate change as predicted. We conclude by suggesting that resurveying historical studies that measured trait frequencies, the strength of selection, or heritabilities could be an efficient way to increase our eco-evolutionary knowledge in climate change biology.

Keywords: climate change adaptation, conservation, dispersal, evolutionary suicide, range dynamics, range shift

Introduction

Climate change is already affecting species worldwide and could cause hundreds of thousands of species extinctions in the future (Urban 2015, Scheffers et al. 2016). Consequently, hundreds of studies are predicting how species will respond to climate change, and conservation biologists are relying on those predictions to guide their



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work. Making accurate predictions by accounting for biological mechanisms is therefore critical to ensure conservation biologists do not waste resources on ineffective actions (Dawson et al. 2011, Urban et al. 2016). However, most predictions of species climate change responses ignore a fundamental biological mechanism: evolution. For example, only one of 131 multi-species predictions included in a recent global synthesis of extinction risk under climate change accounted for evolution (Urban 2015, Urban et al. 2016).

Reviews suggest that evolution might only rescue species from extinction in particular cases: if species have short generation times and large population sizes (Bell and Collins 2008, Quintero and Wiens 2013, De Meester et al. 2018). However, evolution to contemporary climate change has already occurred in a variety of species (Merilä and Hendry 2014, De Meester et al. 2018), and evolution could affect ecological responses of many species even if it does not rescue them from extinction. Evolution could even hasten some extinctions (Box 1; Travis et al. 2010). Climate change could also increase evolutionary potential (Box 2) and cause evolution in a number of ways (Box 1), and these different modes of evolution can interact with each other and ecology to produce complex eco-evolutionary dynamics under climate change (Norberg et al. 2012, Gilbert et al. 2018, Thompson and Fronhofer 2018). We therefore need to understand eco-evolutionary dynamics under climate change to make accurate predictions and employ efficient conservation actions.

Here, we discuss how evolution could alter ecological responses to climate change on species warm and cool range margins where evolution could be particularly important for several reasons. First, range-margin populations might be most likely to evolve under climate change because they are often the first to experience novel selection. Second, range-margin populations are often genetically unique and diverse, which makes them conservation targets and potentially crucial for species persistence in future climates (Hampe and Petit 2005, Rehm et al. 2015). Third, species commonly respond to climate change via range shifts and therefore many ecological predictions and climate change conservation strategies focus on range margins (Davis and Shaw 2001, Heller and Zavaleta 2009, Schmitz et al. 2015). Last, many species' range margins are not shifting as predicted under climate change (Chen et al. 2011, Sunday et al. 2012, MacLean and Beissinger 2017). Evolution might explain these anomalies.

We build on previous reviews (Hill et al. 2011, Travis et al. 2013, Hargreaves and Eckert 2014, De Meester et al. 2018) by: 1) considering interactions among multiple evolutionary processes, 2) highlighting how eco-evolutionary dynamics could alter common ecological predictions and 3) discussing conservation implications. We first take a single species perspective, but then discuss how multiple species affect eco-evolutionary dynamics. For conservation implications, we focus on four of the most recommended conservation strategies (Heller and Zavaleta 2009, Schmitz et al. 2015): 1) increasing landscape connectivity, 2) assisted migration

or gene flow, 3) preserving climate change refugia and 4) monitoring. We provide an eco-evolutionary perspective that could improve these sometimes contentious strategies. We conclude by suggesting a way to rapidly increase our understanding of when, where and how evolution will be important under climate change.

Single species eco-evolutionary dynamics

Cool range margins

As climates change, climates beyond the cool range margin will often become suitable allowing species to expand their ranges. Theoretically, range expansion rates are determined by dispersal propensity, dispersal distance and population growth rate on the expanding range front (Kot et al. 1996, Weiss-Lehman et al. 2017). Low dispersal propensity, short dispersal distance, or slow population growth rate in range-front populations might slow range expansion, which could make many species vulnerable to climate change (Loarie et al. 2009, Sandel et al. 2011, Schloss et al. 2012, Nadeau and Fuller 2016). Evolution could mediate these factors, cause unexpected patterns of range expansion for many species and explain why some species are tracking suitable climates better than others under contemporary climate change (Chen et al. 2011, Sunday et al. 2012, Estrada et al. 2015, MacLean and Beissinger 2017).

Spatial sorting and natural selection could cause population growth rate and dispersal to evolve during range expansion and allow some vulnerable species to track suitable climates. Spatial sorting occurs when individuals with high dispersal propensity or ability are the first to colonize habitats made newly suitable by climate change, which creates populations of highly dispersive individuals on the range front (Box 1; Travis and Dytham 2002, Shine et al. 2011). Natural selection can favor individuals with higher fecundity or dispersal ability on the expanding range front because range-front populations are often released from intra- and inter-specific tradeoffs that constrain this evolution in the range center (Burton et al. 2010, Gilman et al. 2010, Phillips et al. 2010a, Svenning et al. 2014). Simulations combining spatial sorting and natural selection suggest that evolution of dispersal-related traits can allow species to track changing climates and overcome dispersal barriers (Travis et al. 2010, Henry et al. 2013, Bocedi et al. 2014). Lab experiments also demonstrate dispersal evolution during range expansion and suggest evolution of dispersal and population growth rate can occur in three to four generations under idealized lab conditions (Fronhofer and Altermatt 2015, Williams et al. 2016, Ochocki and Miller 2017, Szűcs et al. 2017, Weiss-Lehman et al. 2017, Van Petegem et al. 2018). Furthermore, dispersal evolution has been observed during range expansions in natural systems for invasive species (Phillips et al. 2010b, Lombaert et al. 2014, Van Petegem et al. 2016) and for species responding to climate change (Hill et al. 1999,

Simmons and Thomas 2004, Bridle et al. 2014). Taken together, evidence suggests that dispersal evolution could accelerate climate-induced range expansions for many species vulnerable to climate change.

However, even if species can disperse fast enough to track suitable climates, they will often encounter novel abiotic and biotic conditions in their new range. Novel conditions could be beneficial or detrimental to range expansion depending on how they affect population growth. Species can rapidly adapt to novel conditions that reduce population growth assuming

sufficient genetic variation on the expanding range front. For example, multiple butterfly species evolved new host-plant preferences that allowed them to colonize new habitats under climate change (Parmesan et al. 1999, 2015, Bridle et al. 2014, Buckley and Bridle 2014). Also, plants are evolving earlier flowering time and increased herbivore resistance to cope with shorter growing seasons and novel herbivores in their newly expanded ranges (Lustenhouer et al. 2017, Macel et al. 2017). The blue-tailed damselfly *Ischnura elegans* also evolved broader thermal tolerances to cope with increased

Box 1. How will climate change cause evolution?

Evolution is commonly perceived as a gradual process of natural selection acting on genetic variation to increase the frequency of the fittest genotypes over many generations (Fig. 1A). Consequently species with long generation times are not expected to evolve under climate change. However, climate change can cause evolution in just one generation, occur without natural selection, and result in adaption or maladaptation (Fig. 1). Moreover, species with long generation times can evolve, even when that evolution does not produce the optimal trait or rescue the population from extinction (Fig. 1A). Considering these additional evolutionary mechanisms and outcomes is necessary to understand eco-evolutionary dynamics under climate change. Here, we highlight five ways that climate change could cause evolution.

Mass mortality

Extreme events such as intense hurricanes, floods, heat waves and droughts, are increasing under climate change (Intergovernmental Panel on Climate Change 2014) and can impose strong selection, especially through mass mortality events (Fig. 1B; Fey et al. 2015). Selective mass mortality can result in rapid adaptation to future climates for even long-lived species (Gehring et al. 2017, Donihue et al. 2018). Even non-selective mass mortality can result in evolution by changing population densities and select for different life histories (Vincenzi et al. 2014). In contrast, mass mortality might lower genetic variation or result in maladaptation that hastens extinctions.

Gene flow

Many species are a collection of highly differentiated populations due to local adaptation and genetic drift. Gene flow among differently adapted populations can rapidly alter gene frequencies (Fig. 1C). Indeed, movement of pre-adapted genotypes poleward or up in elevation is one of the primary ways species will respond to climate change. However, preadapted genotypes may not exist to replace warm-margin populations and not all preadapted genotypes are located near their future suitable climates (Rehfeldt et al. 2002). In some of these cases, gene flow might still aid local adaptation by increasing genetic variation (Barton 2001, Sexton et al. 2011, Kremer et al. 2012, Polechova 2018). In other cases, gene flow might result in maladaptation, hindering climate change responses (Kirkpatrick and Barton 1997, Bridle et al. 2009, Paul et al. 2011, Fedorka et al. 2012).

Spatial sorting

Spatial sorting occurs when individuals with high dispersal ability are the first to colonize habitat on expanding range fronts (Shine et al. 2011). Poor dispersers are less likely to reach the range margin, leaving good dispersers to mate with one another and produce even better dispersers in the next generation (Fig. 1D). Spatial sorting has the potential to increase the ability of species to shift their ranges in response to climate change and has already been observed in some species (see Single species eco-evolutionary dynamics on cool range margins).

Genetic drift

Genetic drift causes evolution due to chance breeding or mortality events in small populations (Fig. 1E). Climate change is decreasing species abundances and fragmenting habitats, both of which could result in small populations susceptible to genetic drift. In addition, populations on expanding range margins are often small and subject to drift. Genetic drift could slow range expansions by reducing population growth rate on range margins or hasten some extirpations or extinctions (see Single species eco-evolutionary dynamics on cool range margins).

Introgression

Introgression is the transfer of genetic material between species due to hybridization and then backcrossing (Fig. 1F). As species shift their ranges they are likely to encounter similar species with which hybridization is possible (Hamilton and Miller 2016, Scheffers et al. 2016). Hybridization can be maladaptive, but it can also facilitate the transfer of beneficial genes that could allow species to adapt to climate change. For example, snowshoe hares *Lepus americanus* in areas with no winter snow cover acquired a gene from jack rabbits *L. californicus* that causes hares to produce brown fur in the winter, which decreases predation risk in areas with no winter snow cover (Jones et al. 2018).

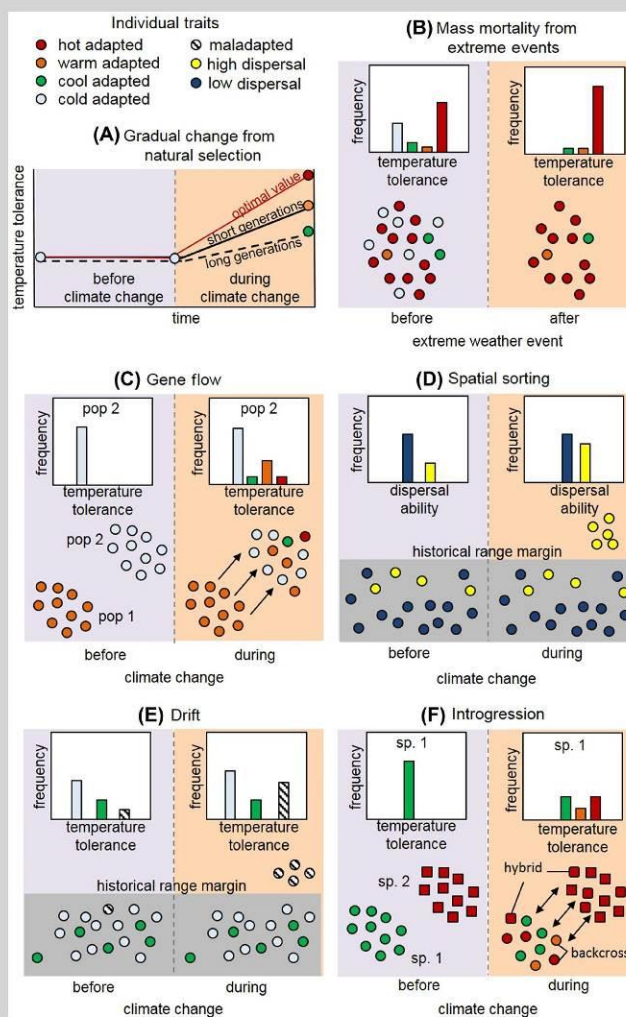


Figure I. Climate change can cause evolution in many ways. Colored circles represent individuals with different traits and groups of symbols represent populations. (A) Gradual changes in the mean temperature tolerance within a population due to natural selection. Red line shows the optimal trait value. Black lines show the change in the mean of a temperature-related trait within a population due to climate change for species with long and short generation times. The colored circles show the mean temperature tolerance of the population at different time periods. (B) Rapid evolution due to selective mass mortality caused by an extreme weather event. In this example, cold adapted genotypes are lost from the population after the extreme event. (C) Rapid evolution in a population due to gene flow between two locally adapted populations: pop 1 and pop 2. Mating among differentially adapted genotypes also produces novel genotypes not present in either population before climate change. (D) Evolution of dispersal due to spatial sorting of individuals with different dispersal abilities. Individuals that disperse further are the first to form populations in newly suitable climates beyond the historical range margin. These highly dispersive individuals mate with one another due to their proximity in space, which maintains high dispersal or produces even better dispersers. (E) Maladaptive evolution due to genetic drift in small populations that form in newly suitable climate beyond the historical range margin. Maladaptive traits arise from dispersal of maladapted individuals from the historical range, or from deleterious mutations. These traits are maintained in the newly formed population by chance breeding and mortality that overcome the effects of natural selection in small populations. (F) Introgression between two closely related species (sp. 1 and sp. 2) that did not encounter one another before climate change. During climate change, species 1 invades the range of species 2. Species 1 and 2 produce hybrids which then move back to species 1's original patch and introduce warm-adapted genes through backcrossing.

Box 2. Shifting evolutionary potential under climate change

The potential for species to evolve under climate change is related to the amount of phenotypic variation within populations, the heritability of those phenotypes and the strength of selection. Measurements of each of these factors under current conditions often suggest the potential for evolution. For example, an ectotherm's upper thermal tolerance can vary by several degrees Celsius within and among populations (Araújo et al. 2013), genetic variation explains 28% of this trait variation on average (Diamond 2017), and individuals with higher thermal tolerances will often be favored under climate change. Climate change could also reveal hidden evolutionary potential even when there is seemingly little potential under current conditions (Schlichting 2008, Husby et al. 2011, Shama 2017).

Our understanding of future evolutionary potential usually rests on a measurement of the proportion of phenotypic variation in a population due to additive genetic variation (i.e. heritability). Heritabilities are useful under constant conditions, but could misrepresent evolutionary potential in the wild for two reasons (Visscher et al. 2008, Hendry 2017). First, heritabilities change as environments change, populations evolve, new mutations arise and immigrants introduce new genes (Lynch and Walsh 1998, Husby et al. 2011). Second, heritabilities differ among populations and environments (Hoffmann and Merilä 1999), yet most heritability estimates derive from a few populations and under restrictive environmental (often laboratory) conditions. Heritability can therefore be high in nature or the future, even when experiments suggest it is currently low (Santos et al. 2012, Heerwaarden et al. 2016, Shama 2017).

Similarly, climate change might expose new genetic variation in many species that could facilitate evolution. Many species harbor cryptic genetic variation, which occurs when multiple genotypes produce the same phenotype under typical conditions (Schlichting 2008, Paaby and Rockman 2014). These cryptic genotypes can produce remarkably different phenotypes under novel environments or new genetic backgrounds (Schlichting 2008, Paaby and Rockman 2014). Climate change is likely to produce novel environments by creating climates without a historical analogue and new species assemblages (Williams and Jackson 2007, Nadeau and Fuller 2015, Pecl et al. 2017). Climate change will also create new genetic backgrounds as genotypes and related species interact, increasing the likelihood of hybridization and introgression (Box 1).

Shifting evolutionary potential under climate change could significantly increase the effects of evolution on species climate change responses. Understanding how and when evolutionary potential will change is therefore critically important. Hundreds of studies have measured phenotypic variation and heritabilities within populations. Repeating these historical studies might be an efficient way to learn where, when and how evolutionary potential is changing under climate change (Box 3).

temporal climate variability in its new range (Lancaster et al. 2015, 2016, Dudaniec et al. 2018). How often species adapt to novel conditions depends on a number of costs and constraints (reviewed by De Meester et al. 2018) and might be most likely early in the range expansion process due to negative genetic effects caused by range expansion.

Range expansions can negatively affect the genetics of range-front populations in two ways (Excoffier et al. 2009). First, repeated founder events and genetic drift in small, newly established populations on the range front can reduce genetic variation (Phillips 2012, Polechova 2018). Many species have reduced genetic variation on their cool range margin due to past range expansions (Hewitt 2000, González-Martínez et al. 2017, Pironon et al. 2017, Willi et al. 2018), and experiments demonstrate that this low genetic variation can limit responses to selection in newly colonized locations (Pujol and Pannell 2008). Also, simulations suggest range-front populations are less likely to adapt to novel conditions encountered later in the range-expansion process when genetic variation is lower (Phillips 2012). Second, deleterious mutations can accumulate on the expanding range front if early colonizers bring deleterious alleles or if genetic drift in small, range-front populations increases the frequency of deleterious mutations (Box 1). Once established on the range front, deleterious alleles can move with the expanding front in a process known as gene surfing (Excoffier et al. 2009). Deleterious alleles can reduce fitness of range-front populations, which can slow range expansion and adaptation to novel conditions. Several models have demonstrated deleterious gene surfing and

its effects on range expansion (Peischl and Excoffier 2015, Peischl et al. 2015, Gilbert et al. 2017, 2018). Moreover, deleterious mutations often persist on range margins during experimental range expansions (Bosshard et al. 2017, Weiss-Lehman et al. 2017) and on cool range margins after historical range expansions in nature (González-Martínez et al. 2017, Willi et al. 2018). Deleterious mutations might also have decreased the range-front fitness of the annual plant *Draba aizoides*, which recently expanded its range due to climate change (Lustenhouwer et al. 2017). Both low genetic variation and a high frequency of deleterious alleles can persist in range-front populations for many generations (Hewitt 2000, Gilbert et al. 2018) in part because genotypes first arriving on the range front can monopolize habitat and prevent colonization of other genotypes (Hewitt 2000, Van Doorslaer et al. 2009a, Atkins and Travis 2010, Kuparinen et al. 2010). If these deleterious consequences of range expansion are common, current range expansions under climate change could slow in the future or even get set back by the collapse of marginal populations (Lynch et al. 1995, Peischl et al. 2015, Gilbert et al. 2018).

No model or experiment has yet evaluated how dispersal evolution, adaptation to novel conditions, reduced genetic variation and deleterious gene surfing might interact to affect range expansions under climate change. Combinations of the potential eco-evolutionary dynamics described above are thus not well understood. However, three models suggest that range expansions might sometimes occur in a three-step pattern involving each of the eco-evolutionary effects described

Box 3. Evolutionary resurveys

Repeating historical studies on trait frequencies, the strength of selection, and heritabilities could be the most efficient way to learn how and when evolution will be important under climate change. Here, we describe three types of evolutionary resurveys to highlight the diversity of possible methods and outcomes.

Resurrecting the past

Many species have resting stages that can persist in sediment or labs for hundreds of years (Hairston et al. 1995, Orsini et al. 2013). These time capsules offer exciting resurvey opportunities with great potential for improving our understanding of evolution in response to climate change (Orsini et al. 2013, Geerts et al. 2015, Franks et al. 2016). For example, researchers recently resurrected

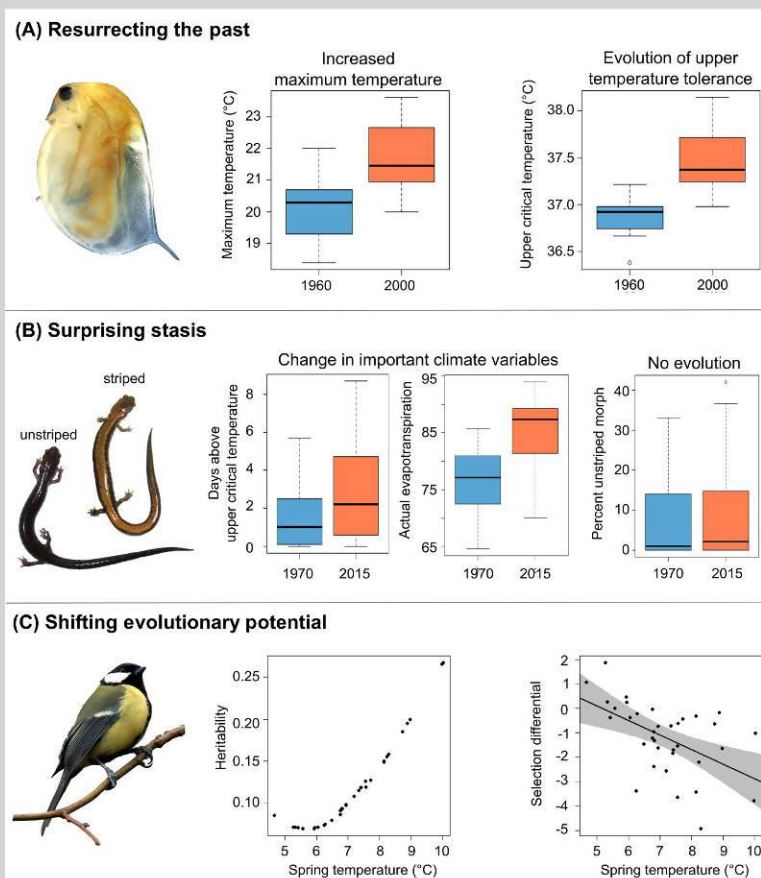


Figure 11. Three examples of rapid learning from evolutionary resurveys. (A) Resting-stage eggs of *Daphnia magna* resurrected from two time periods 1955–1965 and 1995–2005 show evolution of upper critical temperature (right panel) due to increases in maximum temperature of the warmest month (left panel) over the 40-year period (data from Geerts et al. 2015). (B) A resurvey of morph frequency in eastern red-backed salamander in New England, USA shows no evolution, despite significant changes in biologically relevant climate variables (data from Evans et al. 2018). (C) Heritability and the strength of selection are higher under warmer spring temperatures for a great tit population in the Netherlands, suggesting increased evolutionary potential under climate change (data from Husby et al. 2011). In (A) and (B), boxes represent the interquartile range, the whiskers represent the values 1.5 times the interquartile range, outliers are displayed with dots and the solid horizontal lines represent the median. In the right panel of (C) the black line and grey shading represent the predicted relationship and 95% confidence interval from a linear regression.

40-year old eggs of *Daphnia magna* – a keystone aquatic crustacean – from the layered sediment of a natural pond (Geerts et al. 2015). They hatched the eggs in the lab and demonstrated significant evolution in upper thermal tolerances over the last 40 years by comparing resurrected and current populations (Fig. IIA). This direct evolutionary test was the first to document evolution of upper thermal tolerances due to climate change in the wild.

Surprising stasis

The eastern red-backed salamander *Plethodon cinereus* is a terrestrial salamander with two genetically determined color morphs characterized by the presence or absence of a dorsal stripe (Fig. IIB; Highton 1959, 1975). Unstriped morphs are thought to be cold intolerant and have lower metabolic rates that might allow them to occupy drier habitats (Lotter and Scott 1977, Fisher-Reid et al. 2013, Evans et al. 2018). Evolution of increased unstriped frequency could therefore help this climate-sensitive species cope with increased future temperatures and higher evapotranspiration. However, a recent resurvey of morph frequencies throughout New England suggests no recent evolution, despite significant changes in important climate variables since the 1970s when the original surveys were completed (Fig. IIB; Evans et al. 2018). This surprising lack of evolution, and other cases like it, will be important for understanding when and where we should expect evolution in nature.

Shifting evolutionary potential

In addition to documenting evolution, resurveys can determine how climate change is affecting the strength of natural selection and trait heritabilities, two primary factors for predicting evolutionary change (Box 2). A long-term nesting survey of great tits *Parus major* in the Netherlands suggests that both heritability of and selection on nesting phenology are higher under warmer spring temperatures (Fig. IIC; Husby et al. 2011). Hence, selection and heritability could increase under climate change, thereby facilitating evolution. If increasing heritability and selection is common, evolution could occur quicker than expected under climate change. Resurveys of heritability and selection will shed light on this important question.

above (Fig. 1; Phillips 2012, Peischl et al. 2015, Gilbert et al. 2018). First, species expand their ranges rapidly, sometimes through the evolution of increased dispersal. In some cases, high dispersal could even maintain sink populations beyond the range of suitable climate (Henry et al. 2013). Second, rapid expansion can result in small, genetically impoverished and potentially maladapted populations on the expanding range front, which can slow the range expansion. Low population growth and the accumulation of deleterious alleles could also cause the collapse of marginal populations in some cases. Evolution might also favor decreased dispersal during this phase due to the high cost of dispersing into unsuitable conditions beyond the range margin (Phillips 2012), which could also set back range expansions if the high dispersal was maintaining sink populations on the range front (Henry et al. 2013). Third, the now slowed range expansion could provide time for population growth, beneficial mutations, and gene flow. Larger populations on the range margin reduce the effects of genetic drift and, although gene flow might reduce local adaptation, there are also positive effects of increased genetic variation (Barton 2001, Sexton et al. 2011, Polechova 2018, Bontrager and Angert 2019). Once the range-front population is large enough and has adapted to novel conditions the cycle might begin again. These eco-evolutionary dynamics could cause a stop-and-go expansion pattern for some species, which could slow some range expansions if the time it takes to adapt to local conditions and overcome the genetic effects of range expansion outweigh the positive effects of dispersal evolution (Fig. 1; Phillips 2012, Gilbert et al. 2018). If this stop-and-go range pattern is common under climate change, then the many range expansions we have observed so far might simply be the rapid expansion phase of this eco-evolutionary cycle and a future

slow-down is possible. More research is needed to understand if this theoretical expansion cycle occurs in nature and how the genetic effects of range expansion tradeoff with dispersal evolution and adaptation.

Warm range margins

Climate change on warm range margins will generate different evolutionary pressures than on cool margins. As climates change, populations on warm range margins will often experience climates found nowhere else in their range. These novel climates can exceed tolerances of warm-margin populations, and preadapted genotypes are unlikely to occur elsewhere in the species range to replace increasingly maladapted populations. Consequently, many studies predict warm margin contractions (Walther et al. 2002, Colwell et al. 2008). However, evolution might be likely on warm range margins due to habitat isolation (Fig. 2) and thus alter how warm-margin populations respond to climate change (Fig. 3).

Biologists often assume that gene flow from a more abundant range center will swamp local adaptation on the less-abundant margin (i.e. the abundant-center hypothesis; Pironon et al. 2017). In addition, small population sizes at the range margin might increase inbreeding, genetic drift and stochastic extirpation (Blows and Hoffmann 2005, Eckert et al. 2008). Consequently, marginal populations are often thought to be small, genetically impoverished, maladapted and prone to extirpation, making evolution on warm range margins seem unlikely. However, meta-analyses fail to support predictions from the abundant-center hypotheses or find weak relationships (Sagarin and Gaines 2002, Eckert et al. 2008, Pironon et al. 2017). In nature, local environmental heterogeneity can produce patchy, isolated populations on range

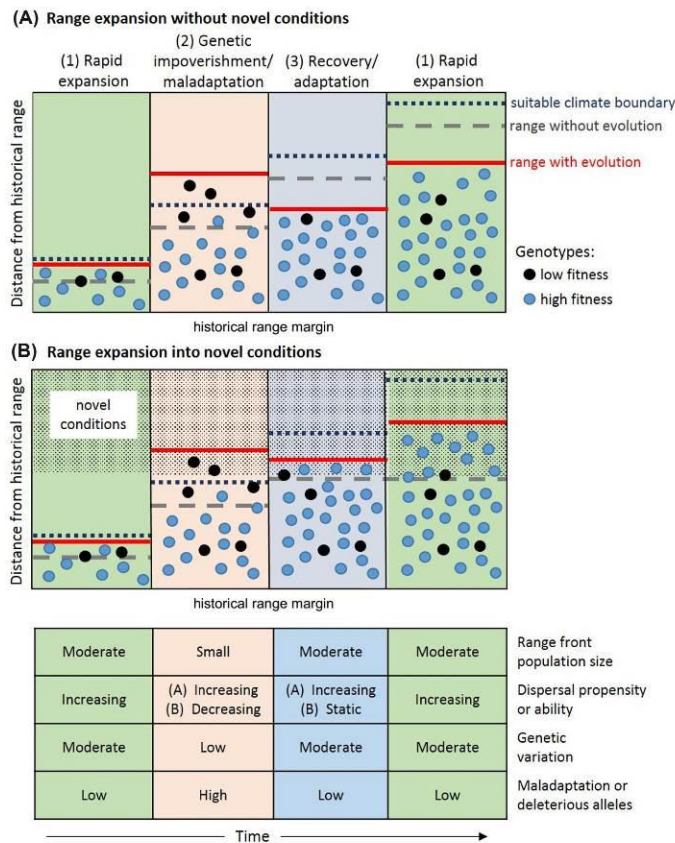


Figure 1. Two examples of how range expansions might proceed when evolution of dispersal, local adaptation and the genetic consequences of range expansion are accounted for, including: (A) when the species does not encounter novel conditions and (B) when the species encounters novel conditions which cause negative population growth rate in the absence of evolution. The horizontal lines show the boundary between suitable and unsuitable climate (blue dotted), the range boundary with evolution (red solid) and the range boundary without evolution (grey dashed). Blue dots represent individuals in the population with high fitness and black dots represent individuals with lower fitness due to maladaptation or deleterious mutations. Without evolution, models assume species will steadily track suitable climates through time, albeit with some lag due to dispersal limitations (distance between grey and blue-dotted lines). However, novel conditions to which the species is maladapted could act as a dispersal barrier and halt range expansion without evolution (B). With evolution, range expansion could occur in a 3-step cycle: 1) species expand their ranges rapidly, often through the evolution of increased dispersal that could increase range expansions relative to a no-evolution scenario. 2) Rapid expansion results in small, genetically impoverished populations on the expanding range front, some of which could occur beyond the range of suitable climate due to high dispersal. Small range-front populations could accumulate deleterious alleles that reduce fitness (both (A) and (B)) or be maladapted to novel conditions (B), which could slow or halt range expansion. In the case where populations experience novel conditions, dispersal can evolve back to pre-expansion levels during this stage due to the high cost of dispersing into unsuitable habitat. 3) The slower range expansion provides time for population growth, beneficial mutations and gene flow that can reduce the effects of deleterious mutations ((A) and (B)) or facilitate adaptation to novel conditions (B). However, populations that occurred beyond the range of suitable climate may also collapse, setting back the range expansion. Once the range-front population is large enough and has adapted to novel conditions the cycle might begin again. When species do not encounter novel conditions, the genetic consequences of range expansion could reduce range expansion rates relative to a no-evolution scenario, although this depends on tradeoffs between dispersal evolution and the genetic consequences of range expansion ((A); see main text). When species encounter novel conditions that act as a dispersal barrier, evolution could facilitate much greater range expansion than expected without evolution (B).

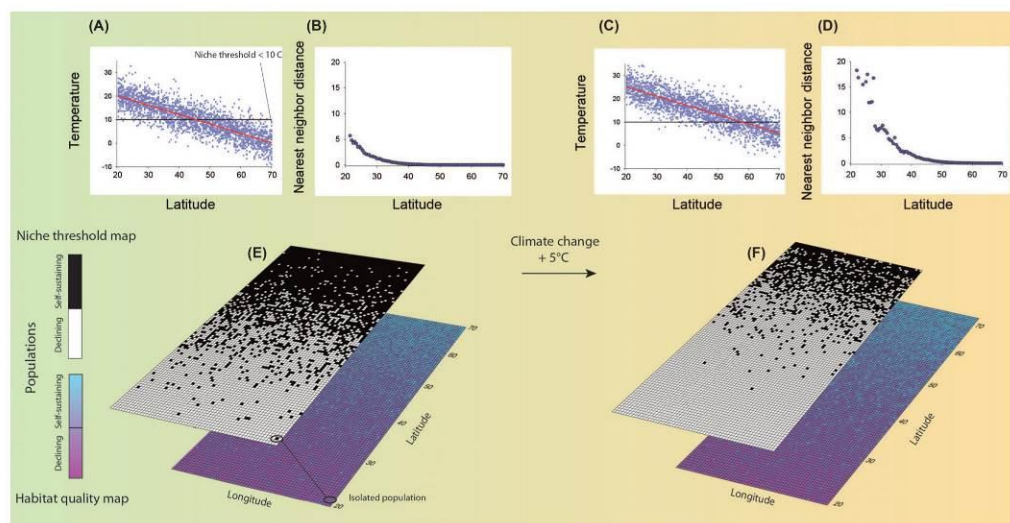


Figure 2. Populations on warm range margins are often isolated (A, B, E) and climate change will increase this isolation (C, D, F). We simulated a 60 by 100-cell grid and assume a climate gradient from 0 to 20°C (red line in (A)) across 50 degrees of latitude. Each cell in the lower habitat quality map (E, F) is a stochastic realization of this climate gradient plus a normal random variable (mean = 0, SD = 20). We apply a fitness threshold at 10°C, such that populations have positive population growth below this temperature (horizontal line in (A)). Using this threshold, we convert the habitat quality map into the upper map of self-sustaining populations indicated in black. Using this map of self-sustaining populations, we calculate the mean nearest neighbor distance between each population at each latitude (B). This analysis demonstrates how isolation increases along a continuous, but variable, habitat gradient. We then assume climate warming (right) and increase the climate gradient by 5°C (red line in (C)), resulting in a retraction of the suitable habitat (F) and increasing edge isolation (D). This simulation demonstrates how populations are naturally isolated on warm range margins and climate change could increase this isolation.

margins (Holt and Keitt 2000), and climate change will likely increase this isolation on warm range margins (Fig. 2). This isolation limits gene flow from the interior and could allow each warm-margin population to adapt to their local climate (Fig. 3; Legrand et al. 2017). Supporting this expectation, genetic differentiation among marginal populations is common and frequently large (Hampe and Petit 2005, Eckert et al. 2008, Pironon et al. 2017). Also, abundance and inbreeding often do not differ between marginal and center populations and abundance of marginal populations is not always reduced by isolation (Pironon et al. 2017). Hence, differentiation among marginal populations might often be due to local adaptation. Species that persisted in warm-margin refugia during past climate changes might also retain higher genetic variation (Hampe and Petit 2005, Cheng et al. 2014, Pironon et al. 2017). This wellspring of genetic variation within and among warm-margin populations could enable evolution to novel climates.

Warm range margins of many terrestrial species are not contracting as predicted under climate change, possibly because biotic interactions or precipitation are more important than temperature in determining species warm range margins (Thomas and Lennon 1999, Chen et al. 2011, Sunday et al. 2012). We propose an additional hypothesis

based on the potential for evolution on warm range margins: the evolutionary extinction debt hypothesis. Under this hypothesis, species ranges are not contracting because evolution is slowing fitness declines on warm range margins resulting in an extinction debt (Fig. 3B). Evolution is seldom considered a mechanism of extinction debt (Hylander and Ehrlén 2013), but evolution can lengthen the time to extinction by slowing maladaptation. For instance, evolution is predicted to increase the time to extinction for endemic alpine plants in the Austrian Alps under climate change (Cotto et al. 2017). The evolution of sprouting probability under climate change could also reduce population growth rate declines of *Cypripedium parviflorum* (Shefferson et al. 2016). Similarly, brown trout *Salmo trutta* populations on their warm range margin are predicted to decline slower than expected by evolving smaller body size (Ayllón et al. 2016). Although evolutionary extinction debt could happen anywhere in a species range, it is especially important on species warm range margins where evolutionary potential might be high and range stasis could affect ecological responses of other species. Evolution on warm range margins could also be hindered if species pre-adapted to novel climates invade and supplant a focal species on its warm range margin. Therefore, evolutionary extinction debt might be a race between adaptation and

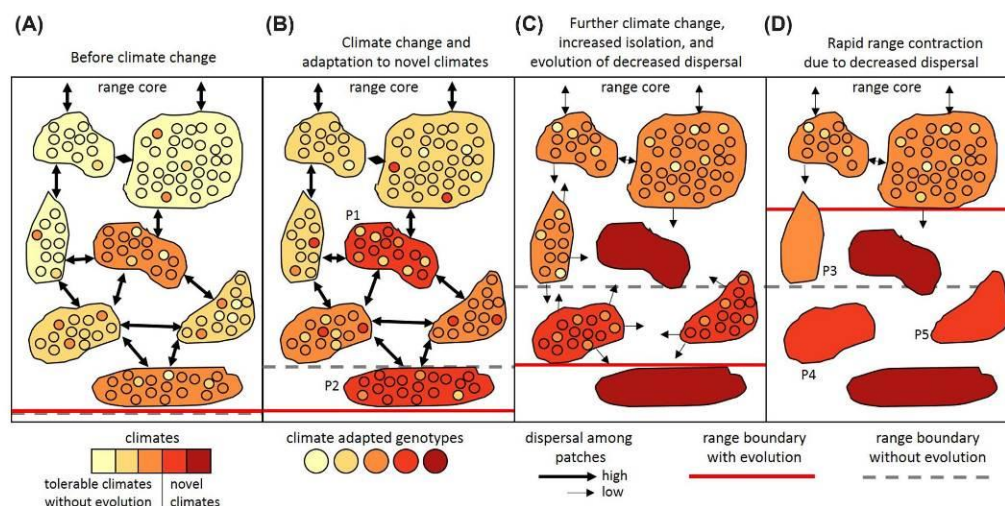


Figure 3. A potential eco-evolutionary model of range contraction on species warm range margins caused by evolution of climatic tolerances and subsequent evolution of decreased dispersal. Each colored polygon represents a patch of potential habitat on the species warm range margin, where the color of the patch represents the climate. The dots represent differently adapted individuals and their color represents the climate they are adapted to. The horizontal lines represent the species warm range margin with (red solid) and without evolution (grey dashed). Before climate change there is high genetic variation in the metapopulation and within patches due to moderate gene flow between locally adapted populations (A). When climates change, the range margin without evolution contracts steadily to track the bottom-most patch that is within the original range of tolerable climates (B and C). With evolution, populations in patches P1 and P2 are initially able to adapt to novel climates and persist, which delays the range contraction (B). When the climates change further, populations in patches P1 and P2 are extirpated, causing a range contraction (C). Extirpations and unsuitable climates cause increased isolation among patches. Consequently, long distance dispersers often land in unsuitable patches and suffer high dispersal mortality which selects for decreased dispersal (C). Stochastic extinctions then occur in patches that remain suitable or where populations have adapted to novel climates (P3–P5). The evolution of decreased dispersal prevents these patches from being recolonized and therefore results in a rapid range contraction (D). In this case, evolution causes a greater range contraction than would be expected without evolution (D), although this will not always be the case.

invasion (Urban and De Meester 2009, De Meester et al. 2016, 2018).

What isolation and evolution provide, however, they might also take away over time. Patches on the warm range margin can become increasingly isolated as climates change (Fig. 2), and pre-adapted species invading and dominating a patch could accelerate isolation. Populations might initially cope with this isolation by evolving increased dispersal (Travis et al. 2010, Williams et al. 2016). Eventually, however, patches can become too isolated and high dispersal mortality can select for decreased dispersal (Comins et al. 1980, Johnson and Gaines 1990, Gros et al. 2006, Travis et al. 2010). Evolving decreased dispersal could cause a rapid collapse of the warm-margin metapopulation if colonizations no longer balance stochastic extirpations (i.e. evolutionary suicide; Gyllenberg et al. 2002, Kokko and López-Sepulcre 2006, Travis et al. 2010, Ferriere and Legendre 2013, Hargreaves and Eckert 2014). Evolutionary suicide could produce a larger range contraction than expected without evolution if stochastic extirpations occur in patches where the population is adapted, and evolution of decreased dispersal prevents these patches from being

recolonized (Fig. 3D). Since selection often reduces population size, stochastic extirpations might increase under climate change and promote this scenario. Few models have evaluated how dispersal will evolve on warm range margins under climate change, and those that do usually exclude a patchy environment necessary to select for decreased dispersal (but see Travis et al. 2010). However, empirical evidence suggests that populations frequently evolve lower dispersal in fragmented landscapes (Cody and Overton 1996, Cheptou et al. 2008, Fresnillo and Ehlers 2008, Riba et al. 2009). Also, high dispersal costs likely caused the evolution of low dispersal in rare endemic plants living in isolated mountain habitats, which increases their extinction risk by preventing them from colonizing new patches (Olivieri et al. 2016). These empirical examples provide evidence that the evolution of decreased dispersal occurs in nature and can affect extinction risk of wild metapopulations.

Taken together, these eco-evolutionary dynamics suggest that high genetic variation on warm range margins could fuel evolution that facilitates population persistence for longer than expected without evolution (Fig. 3B). However, once

populations begin to disappear, increasing isolation could select against dispersal (Fig. 3C), which could cause metapopulation collapse and a rapid range shift (Fig. 3D). Rapid loss of the warm-margin metapopulation could occur unexpectedly after a prolonged period of population persistence aided by evolution. This persist then plummet model of range contraction on species warm range margins could result in surprising and rapid changes that affect entire communities, and therefore has important conservation implications.

Multi-species eco-evolutionary dynamics

Species interactions can affect the eco-evolutionary dynamics discussed above in two key ways: 1) adaptation of a focal species can depend on the presence of other species (i.e. ecology to evolution) and 2) evolution in one species can affect ecological responses of other species (i.e. evolution to ecology). Here we discuss these two possibilities.

Ecology-to-evolution interactions

Species interactions can help or hinder adaptation depending on the type of interaction (Harmon et al. 2009, Van Doorslaer et al. 2009b, 2010). Species interactions can hinder adaptation by reducing the abundance of a focal species or opposing the selection induced by climate change (Johansson 2008, Price and Kirkpatrick 2009, Osmond and de Mazancourt 2013). For example, when predators expand their ranges from lower latitude they often encounter naïve prey that lack defenses and therefore the prey suffer high mortality (Laurila et al. 2008, Urban and Richardson 2015). Increased mortality could cause local prey extirpations or decrease prey abundance, which can limit evolution to both new climates and novel predators. Also, species pre-adapted to novel conditions might often invade and supplant a focal population before it has time to adapt (Norberg et al. 2012), which is especially likely in more diverse communities where pre-adapted species are more likely (de Mazancourt et al. 2008). Experimental tests with mountain plants suggest that novel competitors tracking suitable climates up in elevation can cause fitness reductions to a focal species persisting on its warm range margin (Alexander et al. 2015). However, fitness of the focal species was unaffected by novel competitors encountered during range expansion on the focal species' cool range margin. This asymmetry suggests that novel species interactions might affect adaptation the most on a focal species warm range margin.

Species interactions can also aid adaptation in several ways. Climate change is creating new hybrid zones around the globe, which could increase or decrease adaptation to novel conditions via introgression (Box 1; Hoffmann and Sgro 2011, Hamilton and Miller 2016, Scheffers et al. 2016). Adaptive introgression is an area ripe for future research. Also, novel and existing species interactions can increase selection towards future conditions (Jones 2008, Osmond and de Mazancourt 2013, Tseng and O'Connor 2015,

Osmond et al. 2017). For example, existing and novel predator-prey interactions can accelerate prey adaptation to changing environments under three scenarios: 1) predators preferentially prey on genotypes that become increasingly maladapted as environments change (Jones 2008, Osmond et al. 2017), 2) predation selects for traits that are adaptive under climate change, such as smaller body size (Tseng and O'Connor 2015) and 3) predation increases mortality, which decreases generation times, and therefore increases evolutionary rates (i.e. the evolutionary hydra effect; Osmond et al. 2017). However, these interactions can also reduce abundance, which increases the likelihood of extirpation and genetic drift (Osmond and de Mazancourt 2013, Osmond et al. 2017). Whether these interactions will accelerate evolution in nature is therefore unknown.

Evolution-to-ecology interactions

Few studies evaluate whether evolution of a focal species affects ecological responses of other species to climate change, yet these evolution-to-ecology interactions could be common. For example, short-lived species can adapt and alter ecological responses to climate change of their longer lived symbionts (Gehring et al. 2017, Torda et al. 2017). We focus on one eco-evolutionary feedback that is particularly important for range dynamics under climate change: evolutionary priority effects. Evolutionary priority effects occur when one species adapts to novel conditions and therefore excludes other species from colonizing new habitat (Urban and De Meester 2009, De Meester et al. 2016). Evolutionary extinction debt on warm range margins could result in such priority effects if species persist for longer than expected on their warm range margins and prevent species at lower latitudes or elevations from tracking their suitable climates (Urban et al. 2012, Thompson and Fronhofer 2018). In extreme cases this could cause a box-car effect, where, like train cars, a whole string of species at lower latitudes or elevations are slowed by stasis of a single species at a higher latitude or elevation (Urban et al. 2011). Simulations suggest that evolutionary priority effects can increase extinction risk of many species (Thompson and Fronhofer 2018). Single-species examples also support this idea: the persistence of maladapted genotypes can prevent invasion by more adapted genotypes under climate change (Hewitt 2000, Van Doorslaer et al. 2009a, Atkins and Travis 2010, Kuparinen et al. 2010).

Similarly, chance evolution of species expanding their cool range margin could provide a substantial barrier to range expansion in some circumstances (Fig. 4). Imagine two species, 1 and 2, co-occur at a joint range boundary by using two separate habitat types. By chance or through better dispersal, species 1 colonizes newly suitable habitat beyond the range margin before species 2. If species 2 arrives late, species 1 could adapt to both habitat types and exclude species 2 by monopolizing the new habitat (Urban and De Meester 2009, De Meester et al. 2016). Species 1 could then continue expanding its range, while species 2 remains in its historical range akin to observed genotypic suture zones following

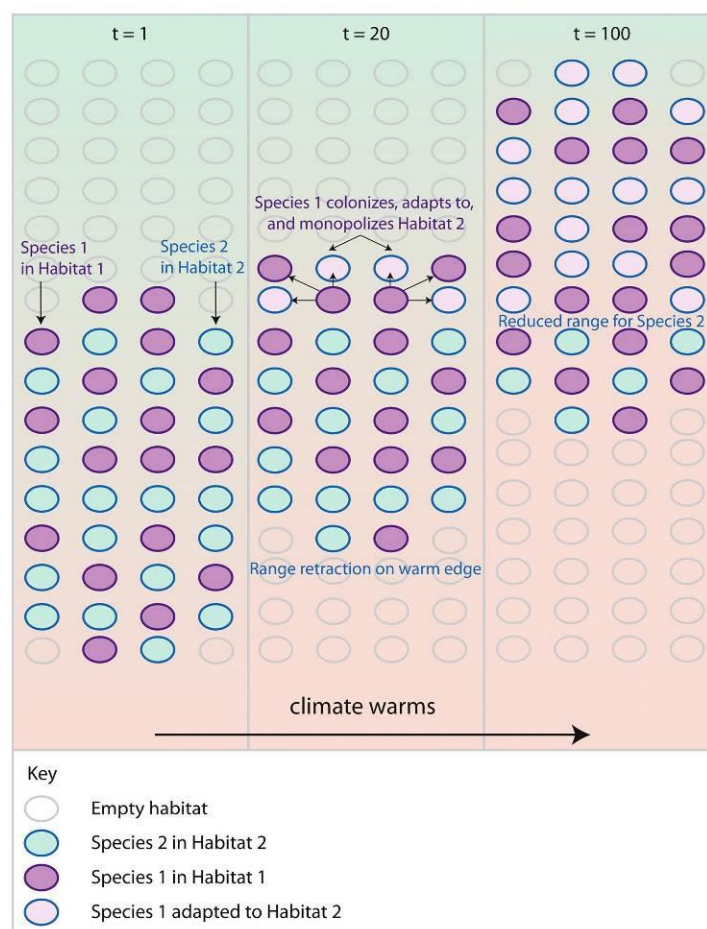


Figure 4. Evolutionary priority effects among species can alter future distributions under climate change. We envision two coexisting species, 1 and 2, each adapted to a different habitat type (habitat 1 and habitat 2). By chance or better dispersal, at $t = 20$ generations (middle), species 1 is the first to colonize a patch of habitat 2 made newly available by climate change. Given sufficient time and genetic variation, it adapts to the new habitat in the absence of species 2 and expands its niche to fill all available habitats. Species 2 is then blocked from shifting its range because species 1 is monopolizing all newly available habitat. Ultimately, as the rear margin retracts, species 2's distribution shrinks and species 1 expands and tracks climate change in both habitats.

postglacial expansion (Hewitt 1999). Predicting such eco-evolutionary dynamics will be difficult because this scenario depends on chance events.

Conservation implications

Eco-evolutionary dynamics present a series of tradeoffs for conservation. For example, accelerating range expansions via assisted migration or increasing connectivity on cool range margins could help species track suitable climates; however,

these conservation strategies might also result in small and genetically impoverished range-front populations that are prone to extirpation (Peischl et al. 2015, Gilbert et al. 2018). Similarly, dispersal corridors up steep environmental gradients might allow species to track suitable climates over short distances, but steep gradients can also prevent adaptation to novel conditions due to high rates of maladaptive gene flow (Kirkpatrick and Barton 1997, Phillips 2012, Polechova 2018). On warm range margins, connectivity between the margin and the species center could allow warm-adapted genotypes to track suitable climates, but connectivity could

also swamp local adaptation and prevent adaptation to novel climates (Sexton et al. 2011). Effective conservation actions must therefore balance these eco-evolutionary tradeoffs.

Species might track suitable climates more successfully on cool range margins if connectivity between current and future suitable locations originates from a variety of locations and does not create spatial bottlenecks. Protecting a corridor of patches in the direction of future suitable climate is a commonly recommended conservation strategy (Robillard et al. 2015). We suggest the use of multiple corridors or corridors that are more than one-patch wide to create multiple possible routes for range expansion (i.e. meta-corridors). Meta-corridors could maintain population differentiation during range expansion, which could increase genetic variation and reduce the effects of deleterious gene surfing in the corridor. Models comparing range expansion in one- and two-dimensional landscapes support this idea: the genetic consequences of range expansion are reduced and fitness recovers faster in two-dimensional landscapes (Peischl et al. 2015, Gilbert et al. 2018).

Similarly, genetic variation and adaptive potential might be increased during assisted migration if individuals from different populations are translocated, especially populations that might be pre-adapted to novel conditions because they come from similar environments to the translocation area (Sexton et al. 2011, Bontrager and Angert 2019). Prober et al. (2015) discuss a number of possible ways to select source populations for assisted migration. However, assisted migration on cool range margins must also consider dispersal evolution. Assisted migration could slow range expansions by disrupting spatial sorting and local adaptation, as demonstrated in three lab experiments (conducted under idealized conditions) that reshuffled individuals within a range (Ochocki and Miller 2017, Szűcs et al. 2017, Weiss-Lehman et al. 2017). Translocating a mixture of highly dispersive individuals and individuals from multiple preadapted populations to newly suitable climates on the cool range margin might therefore be the best approach (Travis et al. 2013). Strong dispersers could help the population continue to expand its range, while genetic variation from multiple source populations could help with adaptation to novel conditions in the translocation area and reduce recovery times from the genetic consequences of further range expansion (Gilbert et al. 2018). Current range-front populations might be a good source for individuals with high dispersal (Travis et al. 2013). Genomics is also being used to determine which species might be best suited for translocation (Fitzpatrick and Keller 2015, Kardos and Shafer 2018), although some authors caution against gene-targeted conservation (Kardos and Shafer 2018), and genomics is not always accessible to conservation agencies (Shafer et al. 2015). On steep environmental gradients, assisted migration beyond the range of maladaptive gene flow from the historical range margin might aid adaptation to novel conditions. Contentious conservation strategies like assisted migration must also consider potential effects on the adaptive capacity of other species.

An eco-evolutionary perspective on warm range margins suggests that maintaining a network of patches (i.e. a metapopulation refugia), rather than a few large high quality patches, could facilitate local adaptation while preventing the evolution of decreased dispersal. Indeed, simulations suggest that preserving only a few large, high-quality patches could lead to the evolution of decreased dispersal and the collapse of the metapopulation (Poethke et al. 2011). Hampe and Petit (2005) suggested maintaining the largest possible number of patches, regardless of their size and quality, which would help maintain metapopulation diversity. However, too much variation in fitness among patches can also lead to the evolution of decreased dispersal (Poethke et al. 2011). High-priority patches should include those buffered against climate change, and we should build accurate models to identify these locations (Keppel et al. 2012, Morelli et al. 2016). Prioritizing an environmentally heterogeneous suite of patches could also help preserve genetic and species diversity (Sgrò et al. 2010, Hoffmann and Sgrò 2011). Ensuring patches are within the dispersal distance of focal species will help balance colonization and extirpation. In some cases, assisted recolonization of extirpated patches from locations with similar climates might slow invasion by other species and prolong persistence of the metapopulation. Networks of connected patches such as described here are currently providing refugia for Belding's ground squirrels *Urocitellus beldingi* and desert bighorn sheep *Ovis canadensis nelsoni* near their warm range margins (Epps et al. 2006, Morelli et al. 2017). Whether this strategy will be fruitful for other species depends on the rate of climate change, genetic variation of the warm-margin metapopulation, and the probability of detrimental invasions by other species.

Last, changing monitoring strategies could more accurately document climate change impacts on range margins. Documenting climate change impacts is primarily accomplished by monitoring changes in occupancy on range margins (Parmesan and Yohe 2003, Chen et al. 2011). However, if evolution commonly causes extinction debt or if eco-evolutionary dynamics slow range expansions, changes in occupancy could underestimate climate change impacts and delay conservation efforts. Climate change can affect population abundances and genetic variation on range margins despite little change in occupancy (Epps et al. 2006, Ayllón et al. 2016, Cotto et al. 2017). For instance, some alpine plants are predicted to decrease in abundance by approximately 75% by 2100, while only decreasing 10% in occupancy (Cotto et al. 2017). Monitoring abundances or genetic variation, rather than occupancies, could therefore warn of extinction debt or potential population collapses.

Future directions

It is clear that eco-evolutionary dynamics could alter range dynamics under climate change. However, there is still much to learn. Many of the predictions described here originate from theoretical models or lab experiments, and their

simplifying assumptions often remain untested (Travis et al. 2010, 2013, Hargreaves and Eckert 2014). Also, many theoretical models and experiments assume climates (or landscapes in the case of general models) are constant in space and time, dispersal is random, and studies focus on one trait in a single species. Future models should incorporate more realistic climates, multiple traits, different dispersal models, and different types of species interactions, which can significantly change results (Norberg et al. 2012, Phillips 2012, Nadeau et al. 2017). More importantly, theory and predictive models have outpaced empirical work, and existing empirical studies are biased towards plants and arthropods in Europe and North America. We need more empirical research on species of conservation interest in a variety of natural settings to inform conservation.

Given these issues, we suggest evolutionary resurveys as a method for rapid learning across many species and contexts (Box 3). Meta-analyses of evolutionary resurveys will elucidate when and where evolution will be important under climate change. Analogously, repeating historical ecological surveys of species abundances, distributions and phenologies have provided valuable information on ecological responses to climate change (Willis et al. 2008, Tingley and Beissinger 2009, Tingley et al. 2009). Hundreds of historical studies of different species and populations have measured trait frequencies, the strength of selection and trait heritability (Mousseau and Roff 1987, Diamond 2017, Hendry 2017). Repeating these surveys with the same methods could efficiently demonstrate evolutionary impacts and potential under climate change. The entire resurvey could be done simultaneously where historical seeds or eggs are available from lab or natural stocks (Geerts et al. 2015, Franks et al. 2016). Incorporating genomics in evolutionary resurveys (e.g. using museum specimens) could map observed changes in phenotypes to associated genotypes and ensure that phenotypic changes are evolutionary, not plastic (Charmantier et al. 2008, Gienapp et al. 2008, Merilä and Hendry 2014). Additionally, we can begin preserving seeds and eggs now or start new common gardens that can be compared to future populations or repeated under future climates (Etterson et al. 2016). Like all methods, evolutionary resurveys have methodological issues that need to be considered carefully, such as the effect of comparing plant phenotypes from seeds that have been stored in the lab for different lengths of time. However, ecological resurveys have overcome methodological issues and proved their value (Tingley and Beissinger 2009, 2013). Hence, we believe evolutionary resurveys have great potential to rapidly increase our understanding of eco-evolutionary responses to climate change.

Conclusion

Ignoring evolution increases uncertainty in climate change biology and threatens to waste limited resources on ineffective monitoring and management. Here we suggest that evolution could increase range expansion rates and allow

populations to adapt to novel conditions on their cool range margins. However, low genetic variation and genetic drift in small range-front populations could also slow or halt range expansions. Meta-corridors could help balance these competing effects of evolution. On warm range margins, adaptation to novel climates could help species persist for longer than expected, although increasing isolation among patches threatens metapopulation collapse. Preserving a network of patches with moderate gene flow on warm range margins might prolong range contractions. These eco-evolutionary dynamics provide hypotheses to explain why many species range margins are not responding to climate change as predicted. Tools now exist to understand and predict evolution and make better informed management decisions despite uncertainty (Dittrich et al. 2016, Hällfors et al. 2016, Urban et al. 2016). We need to apply these tools if we hope to understand and prevent the worst biotic impacts of climate change.

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Chapter 6: Adaptation Overcomes Competitive Dominance and Alters Community Assembly

ABSTRACT

Recent syntheses of ecology and evolution are shedding new light on biodiversity patterns and responses to anthropogenic disturbances. In particular, a growing body of theory predicts that local adaptation of an early-arriving species to a new environment can produce a competitive advantage against later-arriving species, therefore altering community assembly (i.e., the community monopolization hypothesis). Applications of the community monopolization hypothesis are increasing. However, experimental tests of the hypothesis are rare and existing tests do not align with theory. Here we provide a rare experimental demonstration of the community monopolization hypothesis using two species of archaea. We first expose one species to low- and high-temperature environments for ~1620 generations. Populations in the high-temperature treatment evolved a 20.2% higher median performance when grown at high temperature. We then use these differently adapted strains to demonstrate that adaptation reduces the invasion ability of a competitively dominant invader in the high-temperature environment. These results are not only consistent with the community monopolization hypothesis, they suggest that adaptation can overcome competitive dominance to alter community assembly. Hence, community monopolization might be much more common in nature than previously assumed. Our results strongly support the idea that patterns of biodiversity might often stem from a race between local adaptation and colonization of pre-adapted species.

INTRODUCTION

A central challenge in biology is to understand and predict the diversity and abundance of species across space and time (MacArthur 1972, Holt 2009, Leibold and Chase 2017).

Historically, ecologists used the niche concept to explain biodiversity patterns by assuming the environment filtered species according to a set of fitness-related traits (Grinnell 1917, Hutchinson 1957, Leibold and Chase 2017). However, for a particular environment to filter species, species need to access that environment via dispersal, and thus a next generation of theories suggested a tension between regional dispersal and niche-based processes (MacArthur 1972, Hanski and Hanski 1999, Leibold and Chase 2017). More recently, Hubbell and others offered a neutral perspective, where stochastic processes determine biodiversity patterns and niches are unimportant (Hubbell 2001, Muneeppeerakul et al. 2008). Despite these competing theories and their recent syntheses (Tilman 2004, Gravel et al. 2006, Leibold and Chase 2017), a meta-analysis of 158 datasets suggests that less than 50% of variation in community composition is explained by environmental and spatial processes (Cottenie 2005, Holyoak et al. 2005). Some researchers even suggest that community ecology is always context-dependent and lacks generalizable laws, especially at the regional scales at which diversity is commonly studied (Lawton 1999). Explaining and predicting patterns of species diversity therefore remains a challenge in biology, especially with increasing human threats to biodiversity.

Recent theories shed new light on this problem with a growing understanding that evolution often acts on short enough timescales to affect ecology (Pelletier et al. 2009, Schoener 2011, Hendry 2017). By combining evolution with the metacommunity concept, the *evolving-metacommunity* framework proposes an integrated role for dispersal, colonization, niche evolution, and species interactions in determining biodiversity patterns (Urban and Skelly 2006, Urban et al. 2008). One idea advanced by this integrative research program is the importance of evolution in priority effects (Fig. 1). A priority effect occurs when the order in which species arrive to a patch alters the structure of communities, usually because the first species to colonize

a location gains a competitive advantage over later arriving species (Figs. 1A and B). Purely ecological priority effects often explain patterns of community assembly, stability, and composition (Shorrocks and Bingley 1994, Symons and Arnott 2014, Fukami 2015). However, evolution can also create or enhance priority effects (Roughgarden 1972). The community monopolization hypothesis predicts that local adaptation of an early-arriving species to a location can produce a competitive advantage against later-arriving species that results in a priority effect (Fig. 1C; Urban et al. 2008, De Meester et al. 2016). Evolution might therefore play an important role in explaining and predicting community assembly.

Indeed, the community monopolization hypothesis has engendered a suite of recent theoretical explorations that suggest evolutionary priority effects could be common in nature (De Meester et al. 2016). Original theory suggested that community monopolization effects were only likely when dispersal probability was low (Loeuille and Leibold 2008) and could be thwarted if pre-adapted species occurred in the metacommunity (de Mazancourt et al. 2008). However, subsequent theory has added a number of complicating factors and demonstrated that evolutionary priority effects can occur under commonly observed dispersal probabilities, when there are pre-adapted species in the metacommunity, in the presence of gene flow, under many landscape structures, and with both sexual and asexual reproduction (Urban and De Meester 2009, Vanoverbeke et al. 2016). Applications of the hypothesis are also providing novel insights about observed adaptive radiations on remote islands (Gillespie 2004, Vanoverbeke et al. 2016), and about the response of biodiversity to environmental disturbances, including climate change (Loeuille and Leibold 2008, De Meester et al. 2016, Thompson and Fronhofer 2019). Most recently, theory has demonstrated how unexplained variation in communities and neutral-like characteristics can arise from evolutionary priority effects (Leibold et al. 2019).

Despite the potential importance and its increasing application, empirical tests of the community monopolization hypothesis are rare. Most experiments and observations supporting the hypothesis fail to demonstrate all three stages (i.e., early arrival, adaptation, and altered community assembly) of the eco-evolutionary process (De Meester et al. 2007, Crutsinger et al. 2008) or test the related single-species version of the hypothesis, the population monopolization hypothesis (De Meester et al. 2002, Fukami et al. 2007). Only one study has demonstrated the dynamic nature of colonization, adaptation, and altered community assembly described by the community monopolization hypothesis. Gomez et al. 2016 demonstrated that community structure in a warm compost environment differed depending on whether an early arriving species, *Pseudomonas fluorescens*, had adapted to the novel environment. However, community monopolization might be favored in this experiment because an entire community containing many species arrived simultaneously after adaptation of the early-arriving species (Gómez et al. 2016). Moreover, the simultaneous arrival of many species is not aligned with theory used to develop the community monopolization hypothesis or its many applications.

Here, we provide a crucial test of the community monopolization hypothesis that is aligned with theory using two species of archaea in the genus *Haloferax*: *H. volcanii* and *H. mediterranei*. We first allow *H. volcanii* to adapt to novel conditions in the lab, and then test whether this adaptation alters the colonization ability of *H. mediterranei*. *Haloferax volcanii* and *H. mediterranei* have on average 84.6% nucleotide identity among shared orthologs (Han et al. 2012) and are estimated to have diverged approximately 80 million years ago (López-García et al. 1995), which is similar to humans and mice (Nei et al. 2001, Mouse Genome Sequencing Consortium 2002). Hence, a test of the community monopolization hypothesis with these two species moves beyond testing the single-species version of the hypothesis. Also, *H. mediterranei*

has characteristics of a “microbial weed”, including the most rapid rate of cell division among halophilic archaeon and broad environmental tolerances (Oren and Hallsworth 2014). These characteristics make *H. mediterranei* a superior competitor in the lab. Hence, evaluating whether adaptation of *H. volcanii* can overcome this competitive dominance and alter community assembly provides a strong and novel test of the community monopolization hypothesis.

METHODS

Study System and Laboratory Conditions:

Haloferax (Class: *Halobacteria*) is a genus of aerobic, heterotrophic archaea that live in aquatic habitats with between 12% and saturated NaCl, such as the Dead Sea. *Haloferax* are mesophilic, showing optimal growth between 40 and 50°C, where they have one generation approximately every two to four hours. For this study, we used an auxotroph of each focal species: *H. volcanii* strain H98, developed as a uracil and thymidine auxotroph (Charlebois et al. 1987, Wendoloski et al. 2001, Allers et al. 2004), and *H. mediterranei* strain WR646, developed as a uracil and tryptophan auxotroph (Naor et al. 2012). Using these auxotrophs facilitated selective plating to count the relative abundance of each species in mixed cultures (see below). We grew lab populations in rich medium supplemented with thymidine. Except where we state otherwise, we grew lab populations in 2 ml, 96-well plates containing 320 µl of medium, and sealed the plates with adhesive foil. We interspersed wells containing isolated populations with empty wells or wells containing only medium to avoid cross-contamination among isolated populations. Preliminary tests indicated no signs of cross-contamination using these techniques. We kept cultures in exponential phase by transferring 20 µl of homogenized culture from the most recently created plate to 300 µl of fresh medium in a new plate every two to five days.

Experimental Evolution of H. volcanii:

We first created two differently adapted strains of *H. volcanii*. We isolated 12 clones (hereafter “founding populations”) of *H. volcanii* by picking colonies from an agar plate streaked from a stock culture (Fig. 2A). We transferred each colony to 600 µl of medium in a 96-well plate and kept the founding populations at 42°C for 24 days to allow adaptation to the laboratory environment (Fig. 2A). After 24 days, we replicated this initial plate six times in separate 96-well plates. Our design resulted in 72 isolated populations founded from 12 clones (Fig. 2A). We grew these replicate plates at 42°C for an additional eight days prior to randomly assigning half the plates to a low-temperature treatment (42°C) and the other half to a high-temperature treatment (48°C; Fig. 2B). At this time, we also preserved the 12 founding populations used to create the six replicates by combining 25 µl of homogenized culture with 25 µl of glycerol solution containing 14% NaCl and then froze the cultures at -80°C (Fig. 2B). The low-temperature treatment remained constant at 42°C for the remainder of the experiment (Fig. 2B). The high-temperature treatment gradually increased from 42°C to 48°C over 57 days and then remained at 48°C for another 78 days (Fig. 2B). We cycled the plates through four incubators during this time to avoid confounding treatment effects with potential incubator effects. During the final five days, we did not provide populations with fresh medium to allow them to reach stationary phase (i.e., maximum density) and then moved all populations to room temperature to slow further adaptation. We resurrected the founding populations 14 days prior to the end of the adaptation experiment and kept them at 42°C to allow for comparison with the adaptation treatments (Fig. 2B).

Testing for Adaptation:

We tested for divergent adaptation among treatments by evaluating the maximum density achieved by the founding, low-temperature, and high-temperature populations when grown at 42°C and 48°C (Fig. 2C). We first consolidated populations into two new plates: (1) a plate containing the 12 founding populations and the 36 low-temperature populations, which we put in a 42°C incubator; and (2) a plate containing the 36 high-temperature populations, which we put in a 48°C incubator. After one week of growth, we moved all populations to 42°C for 48 hours to provide a common acclimation temperature. We then split both plates into two identical replicates by transferring 20 µl of homogenized culture into 80 µl of medium in 96-well optical plates. We also included 12 wells in each optical plate that contained 100 µl of medium only. We sealed each plate with transparent plastic film and distributed the plates between 42°C incubator and a 48°C incubator, such that both low-temperature and high-temperature populations were growing at 42°C and 48°C. After nine days, we measured optical density by absorbance of light at 620 nm. Prior to analysis, we averaged optical density from the 12 wells containing only medium in each plate and subtracted the average from all optical density measurements in that plate. We used this final measure of optical density as an assay of performance. We excluded nine populations from our analysis because they did not grow on the final plate used to measure optical density.

We tested for divergent adaptation using a Bayesian mixed-effects model with the ‘*R2jags*’ package in the R statistical software version 3.6.0. We used maximum optical density as the response variable and the following independent variables: treatment (founder, low-temperature, and high-temperature treatments), common-garden temperature (42°C and 48°C), and their interaction. We also included random intercept terms for clone to account for the

replication of clones across plates and treatments, and plate to account for any potential differences among plates within treatments. We used weakly informative normal priors with a mean of zero and a variance of 1000 for all coefficients and a uniform prior ranging between zero and 100 for the standard deviation of the error terms (Gelman 2006). We ran three chains in the MCMC sampling each for 100,000 iterations with a burn-in period of 50,000 iterations and retained every tenth draw, which resulted in well-mixed chains for all parameters (i.e., Gelman-Rubin statistics < 1.01). Posterior predictive checks of the mean and variance of the data suggested the model fit the data well (Bayesian $p_{\text{mean}} = 0.499$, Bayesian $p_{\text{variance}} = 0.553$). We calculated the posterior for all pairwise differences among treatments at each temperature to evaluate adaptation. We considered pairwise differences significant if the 95% credible interval of the difference did not overlap zero.

Testing for Competitive Dominance and Priority Effects:

We tested whether *H. mediterranei* was competitively dominant as predicted by its high growth rate and broad environmental tolerances (Oren and Hallsworth 2014) by allowing populations of *H. volcanii* and *H. mediterranei* to compete at 48°C. We inoculated 160 µl of medium with 20 µl of *H. volcanii* and 20 µl of *H. mediterranei* culture, each with a standardized density of 11×10^5 colony forming units (CFUs) per ml. We replicated these competition experiments using four biological replicates of *H. volcanii* and four biological replicates of *H. mediterranei* in a fully factorial design (i.e., 16 competition experiments). The populations used in these experiments were different clonal lines than those used in the adaptation experiments and in the priority-effect experiments described below.

We tested for ecological and evolutionary priority effects (Fig. 1) by allowing *H. mediterranei* to invade low- and high-temperature adapted populations of *H. volcanii* growing at

the high temperature (48°C). Invasion of *H. volcanii* populations adapted to the low temperature (but growing in the high temperature) represents a scenario where *H. volcanii* arrives first, gains a numerical advantage, but does not adapt to the high temperature (Fig. 1B). Whereas, invasion of *H. volcanii* populations adapted to and growing at the high temperature represents a scenario where *H. volcanii* arrives first and adapts to the high temperature prior to the arrival of *H. mediterranei* (Fig. 1C). The community monopolization hypothesis predicts that the abundance of the second colonist should be lower when it invades adapted populations of the first colonist (Fig. 1).

We conducted the invasion experiments by first inoculating 160 µl of medium with 20 µl of *H. volcanii* culture with a standardized density of 11×10^6 CFUs per ml. We then immediately added 20 µl of *H. mediterranei* culture with a standardized density of 11×10^5 CFUs per ml. This simulated a 10% invasion. We replicated this invasion using eight *H. volcanii* populations from the low-temperature treatment and eight populations from the high-temperature treatment that originated from the same eight founding populations, which created a paired design. The single *H. mediterranei* culture used in these experiments was a homogenized mixture of populations that had been growing at 42°C for 65 days.

We grew mixed-species cultures for 48 hours in a 96-well optical plate placed in a 48°C shaking incubator for both the competitive-dominance and priority-effect experiments. After 48 hours, we measured the abundance of *H. volcanii* and *H. mediterranei* in each community using selective plating. We plated serial dilutions of all communities ranging from 10^{-5} to 10^{-8} onto 100 mm (competitive-dominance experiments) or 50 mm (priority-effect experiments) agar plates created with casamino acids medium supplemented with uracil, and either thymidine and hypoxanthine to allow *H. volcanii* growth or tryptophan to allow *H. mediterranei* growth. After

incubation, we counted the CFUs growing on each plate type, and averaged the results to provide an estimate of density for each species in each of the 32 mixed-species communities. During the priority-effect experiments we also plated a 10^{-3} dilution of a subset of communities on plates lacking both thymidine and tryptophan (but containing uracil) to test for possible mating, recombination, and loss of auxotrophy between congeners that could undermine the efficacy of selective media to facilitate measurement of species-specific abundances (Naor et al. 2012). We observed no growth on uracil-only plates in this experiment, indicating no substantial recombination between species and no contamination of the communities with non-auxotrophic strains.

We used a Bayesian generalized mixed-effects model to test the predictions in Fig. 1. We modeled the proportion of *H. mediterranei* in mixed-species communities from each treatment using a beta regression with a factor identifying the three treatments shown in Figs. 1 and 4. We also included random effects for the *H. volcanii* clones used in all experiments and *H. mediterranei* clones used in the competitive dominance experiments. We used weakly informative priors as described above and a weakly informative gamma prior with shape and scale parameters set to 0.01 for the precision coefficient. We ran three chains in the MCMC sampling each for 250,000 iterations with a burn-in period of 50,000 iterations and retained every tenth draw, which resulted in well-mixed chains for all parameters (i.e., Gelman-Rubin statistics < 1.01). Posterior predictive checks of the mean and variance of the data suggest the model fit the data well (Bayesian $p_{\text{mean}} = 0.514$, Bayesian $p_{\text{variance}} = 0.594$). We calculated the posterior difference among treatments and considered the treatments different if the 95% credible interval of the difference did not overlap zero.

RESULTS

Adaptation to High Temperature:

H. volcanii populations that grew in the high-temperature environment for ~1620 generations adapted to the high temperature. *Haloferax volcanii* populations from the high-temperature treatment had a 21.5% higher median performance than the founding populations (95% CI of the difference in performance = 0.035 – 0.060) and a 20.2% higher median performance than populations from the low-temperature treatment (95% CI of the difference in performance = 0.036 – 0.054) when grown at the high temperature (Fig. 3). Populations from the high-temperature treatment also performed slightly better (5.3% and 6.1%, respectively) than the founding populations (95% CI of the difference in performance = 0.004 – 0.029) and populations from the low-temperature treatment (95% CI of the difference in performance = 0.009 – 0.027) when grown at the low temperature (Fig. 3). In contrast, median performance did not differ between the founding populations and populations from the low-temperature treatment when grown at the low temperature (95% CI of the difference in performance = -0.014 – 0.010) or high temperatures (95% CI of the difference in performance = -0.011 – 0.015), suggesting no evolution in response to lab conditions other than temperature.

Ecological and Evolutionary Priority Effects:

H. mediterranei dominated the community with a median proportion of 0.88 when both species arrived simultaneously to the high-temperature environment at equal abundance (Fig. 4). This demonstrates the competitive dominance we expected in the absence of priority effects. When unadapted *H. volcanii* arrived early and gained a numerical advantage, the proportion of *H. mediterranei* in the community decreased by a median of 45% relative to when the two species arrived simultaneously, demonstrating an ecological priority effect (Fig. 4). The median

difference in the proportion of *H. mediterranei* in the community between these two scenarios was 0.38 (95% CI = 0.11 – 0.54; Fig. 4). When *H. volcanii* arrived early and adapted to the high-temperature environment, the proportion of *H. mediterranei* in the community decreased by a median of 36% relative to when *H. volcanii* did not adapt, demonstrating an evolutionary priority effect consistent with the community monopolization hypothesis. The median difference in the proportion of *H. mediterranei* in the community between these two treatments was 0.17 (95% CI = 0.07 – 0.27; Fig. 4). Overall, early arrival and adaptation resulted in a 65% median reduction in the proportion of *H. mediterranei* in the community (Fig. 4).

DISCUSSION

We provide the first experimental example of an evolutionary priority effect between two highly diverged species. Our results support the growing number of studies that suggest community assembly might often be a race between adaptation of the first colonists and the colonization by pre-adapted species (Roughgarden 1972, Vanoverbeke et al. 2016). Moreover, our work suggests evolutionary priority effects might play a stronger role in nature than previously assumed. Most theory on evolutionary priority effects assumes species are neutral at either the local or metacommunity scale prior to evolution (Urban and De Meester 2009, Vanoverbeke et al. 2016). In nature, however, species often exhibit strong asymmetric competition, which is often thought to negate priority effects (Fukami 2015). Our results demonstrate that evolution can overcome this asymmetric competition and alter community assembly, which significantly broadens the contexts where evolutionary priority effects might be important in nature.

Moreover, by focusing on two highly diverged species, our work builds on prior examples that provided within-species demonstrations of monopolization effects. Within-species

demonstrations might be more likely to result in evolutionary priority effects due to the functional equivalence between the invading and adapted ecotypes given their genetic similarity and rapid evolution of traits caused by simple genetic changes (Spiers et al. 2002, McDonald et al. 2009, Ferguson et al. 2013). Greater differences among highly diverged species might reduce evolutionary priority effects if competing species diverge into separate niches (Bassar et al. 2017) or compete so asymmetrically that no level of adaptation can overcome competition. Here, we demonstrate that evolutionary priority effects occur between two archaeon species that are separated by 80 million years of evolution and as genetically divergent as humans and mice (Nei et al. 2001, Mouse Genome Sequencing Consortium 2002, Han et al. 2012). Our work therefore opens the door for a fuller exploration of evolutionary priority effects among a wide variety of species in natural communities.

Our experiments provide support for a growing number of theoretical, conceptual, and observational studies using evolutionary priority effects to explain biodiversity patterns in nature. For example, recent studies have provided phylogenetic support for the long-held idea that adaptive radiations by initial colonists can affect community assembly (Wilson 1961, Roughgarden 1972, Schluter 2000, Losos and Ricklefs 2009). Plants in the Canary Islands and Macronesia are likely monophyletic because early colonists radiated to fill empty niches and restricted the colonization of other species via niche preemption (Silvertown 2004, Silvertown et al. 2005). Molecular phylogenies and paleo-reconstruction of available niches provide strong support for similar macro-evolutionary priority effects for alpine plants in New Zealand (Lee et al. 2012, Leopold et al. 2015, Tanentzap et al. 2015). Models and phylogenetics also provide compelling evidence that *Tetragnatha* spiders often diversify and monopolize habitat on newly-

formed Hawaiian islands, therefore limiting colonization by other species (Gillespie 2004, Vanoverbeke et al. 2016).

Our results are also relevant to thinking more critically about the joint ecological and evolutionary processes that determine future communities in response to anthropogenic disturbances such as climate change. To date, most predictions of the redistribution of biodiversity under global change take a single-species, niche-focused approach and suggest that many species will simply shift their distribution to track suitable habitat (Hampe 2004, Urban et al. 2016). However, theory has already suggested that the redistribution and loss of biodiversity due to global change might depend on a race between local adaptation and the movement of pre-adapted species (de Mazancourt et al. 2008, Urban et al. 2012, Mokany et al. 2019, Nadeau and Urban 2019, Thompson and Fronhofer 2019). For example, if a species adapts to changing climates in its current range or in newly encountered environments as it expands its range, it could prevent other species from shifting their ranges and lead to higher levels of extinction than predicted without evolution (Atkins and Travis 2010, Nadeau and Urban 2019, Thompson and Fronhofer 2019). Our results demonstrate such eco-evolutionary species interactions due to warming. However, an important next step is to determine how quickly evolution can result in a priority effect. In our experiments, adaptation occurred over ~1620 generations, which is certainly relevant to microbial responses to climate change, but likely too slow to alter climate change responses for species with longer generation times. Observed cases of rapid evolution in response to climate change are accumulating quickly for a wide variety of species (De Meester et al. 2018, Nadeau and Urban 2019). Thus, it seems likely that evolutionary priority effects could occur under climate change and alter species responses.

Highly controlled lab experiments in simple communities like ours are required to demonstrate proof-of-concept, but necessarily exclude important details that could alter results in nature. Future experiments should test how quickly evolution can alter priority effects under different biological contexts such as sexual versus asexual reproduction or with varying levels of genetic diversity (De Meester et al. 2016, Vanoverbeke et al. 2016). Environmental contexts, such as varying degrees of isolation or analogue versus no-analogue environments might also be important (De Meester et al. 2016, Vanoverbeke et al. 2016, Thompson and Fronhofer 2019). Moreover, experiments should evaluate how eco-evolutionary dynamics in mixed-species communities play out over longer timeframes. We only maintained mixed-species communities for 48 hours (~24 generations) and we do not know how eco-evolutionary dynamics would play out over longer timeframes. Indeed, competition for resources over longer timeframes can have complex effects on eco-evolutionary dynamics (Hart et al. 2019). Moreover, co-evolution among species can affect the outcome of invasions (Faillace and Morin 2016, 2020). Continued adaptation to high temperature by *H. volcanii* could result in the eventual exclusion of *H. mediterranei*, which would enhance the results presented here. Alternatively, the evolutionary priority effects we observed could be transient, and eventually *H. mediterranei* could exclude *H. volcanii*. Nevertheless, transient evolutionary priority effects will slow ecological dynamics, which could explain biodiversity patterns in nature, such as why species are often not currently responding to climate change as predicted (Chen et al. 2011, Sunday et al. 2012, MacLean and Beissinger 2017, Nadeau and Urban 2019). Ultimately, the next step in understanding the importance of evolutionary priority effects is experiments in nature with a diversity of taxa (Pelletier et al. 2009, Post and Palkovacs 2009, Hendry 2017, De Meester et al. 2019). Such

experiments will help predict where and when evolution could win the race against colonization by pre-adapted species.

Overall, our results provide experimental support for the idea that the joint processes of dispersal, niche evolution, and local species interactions act together in ways that determine community assembly and ultimately affect the abundances of competing species. Accounting for these interacting processes could alter explanations for observed patterns and predictions in diverse fields of ecology and evolution, including biogeography, community ecology, restoration ecology, and climate change biology (Emerson and Gillespie 2008, Fukami 2015, De Meester et al. 2016). The evolving metacommunity concept, from which the community monopolization hypothesis stems, offers a complementary and synergistic view of the tension between the dominant biodiversity theories ruled by either niche-based determinism or neutral stochasticity. Joining these views suggests that understanding arrival times and adaptation could allow us to forecast outcomes of community assembly and contribute to a more predictive community ecology.

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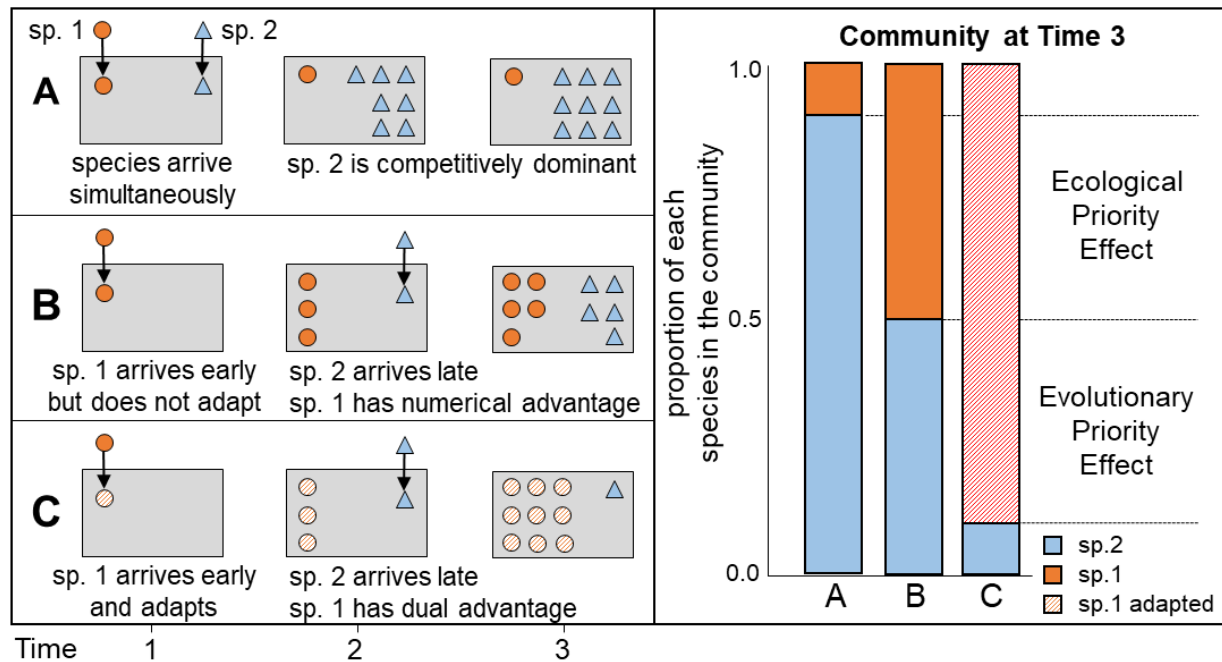


Figure 1. Three examples of community assembly over time (left) demonstrating ecological and evolutionary priority effects. (A) Two species (sp. 1, orange circles and sp. 2, blue triangles) arrive to an open habitat patch (grey square) at the same time. Species 2 has a competitive advantage and therefore occupies a much larger portion of the community in time 3 (bars on right). (B) Species 1 arrives early and gains a numerical advantage prior to the arrival of species 2, which allows species 1 to occupy half the community in time 3. The difference between A and B is an ecological priority effect (right). (C) Species 1 arrives early and adapts to novel conditions in the habitat patch prior to the arrival of species 2. Now, species 1 has a numerical and an adaptive advantage, which allows it to occupy a larger portion of the community in time 3. The difference between B and C is due to an evolutionary priority effect.

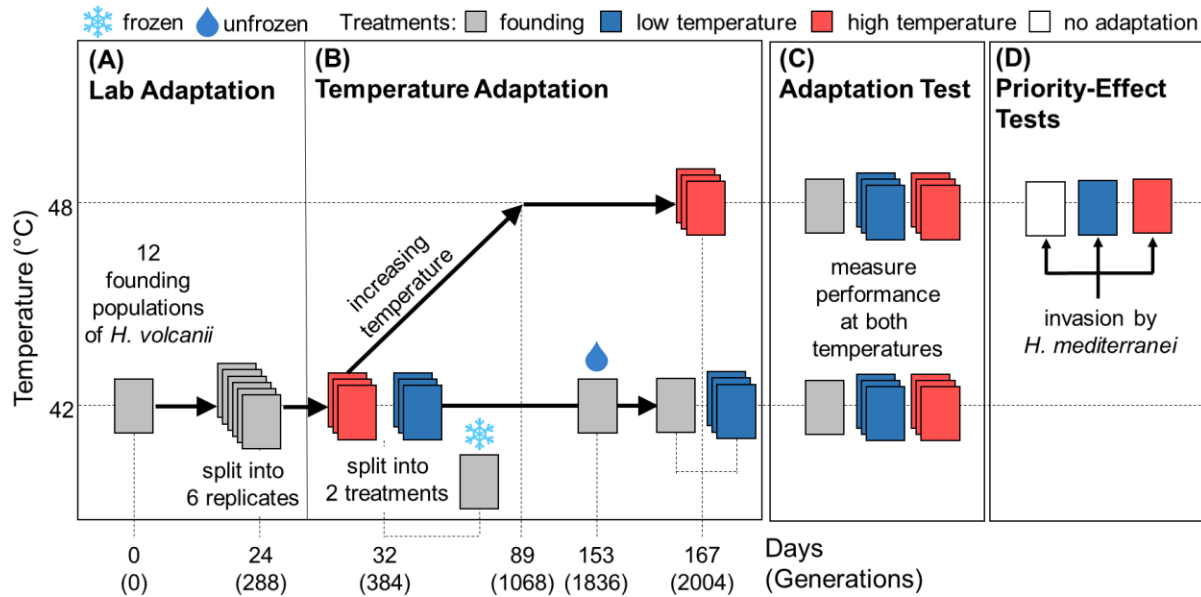


Figure 2. The experimental design used to test for ecological and evolutionary priority effects. (A) We created 12 independent populations of *H. volcanii* (grey) and allowed them to adapt to lab conditions for 288 generations. (B) We then replicated the founding populations six times and split the replicates between two treatments: we placed 36 populations in a high-temperature environment (red), and 36 in a low-temperature environment (blue). We also froze (snowflake) the 12 original founding populations at this time. Populations remained at these temperatures for 1620 generations and we resurrected frozen founding populations (blue drop) 14 days prior to the end of the adaptation period. (C) We then tested for adaptation by measuring the performance of the founding, low-temperature, and high-temperature populations at both the low and high temperature. (D) Last, we allowed *H. mediterranei* to invade differently adapted *H. volcanii* populations growing at high temperature and measured proportional abundance of each species in the mixed communities to test for competitive dominance and ecological and evolutionary priority effects.

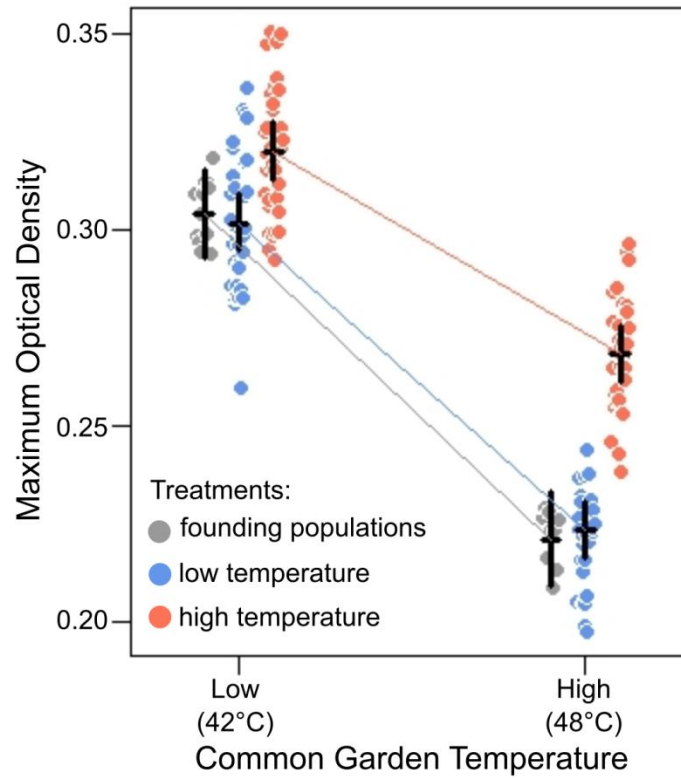


Figure 3. Populations of *H. volcanii* exposed to high temperature for ~1620 generations perform better than founding populations and populations from the low-temperature treatment when grown in the low-temperature (42°C) and high-temperature (48°C) environments. Points show the maximum optical density (a measure of performance) for each founding population (grey dots), each population from the low-temperature treatment (blue dots), and each population from the high-temperature treatment (red dots) when grown at 42°C and 48°C. Black crosses are the median (horizontal line) and 95% credible interval (vertical line) for each group estimated from a Bayesian mixed-effects model.

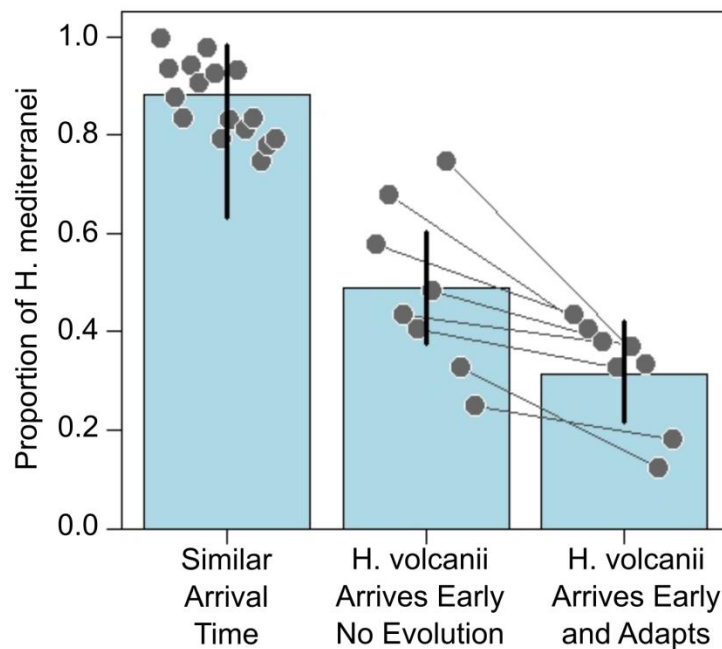


Figure 4. Arrival time and evolution affect community assembly between two species of *Halobacteria* - *H. volcanii* and *H. mediterranei* – when grown in a high-temperature environment. When both species arrive to an open habitat at similar times, *H. mediterranei* is competitively dominant (left bar). However, if *H. volcanii* arrives first and gains a numerical advantage, the proportion of *H. mediterranei* in the population is reduced by a median of 45% (middle bar). If *H. volcanii* arrives first and adapts to the high temperature, the proportion of *H. mediterranei* is further reduced by 36% (right bar), which is the signature outcome of an evolutionary priority effect. The blue bars show the median proportion of *H. mediterranei* 48 hours (~24 generations) after invading populations of *H. volcanii*. Error bars are 95% credible intervals from a Bayesian generalized mixed-effects model. Points show the proportion of *H. mediterranei* in each of the 32 competition experiments. Diagonal lines between points over the right two bars join paired points based on the founding populations of *H. volcanii* used to start the low and high-temperature treatments.